

Original Article

Inheritance of pericarp pigment on crossing between black rice and white rice

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Abstract

This research studied the genetic parameters of the pigment characters of rice. The experiments were conducted in two stages: establishment of base population through crossing between black rice with white rice and F₁s were grown in the green house and F₂ seeds in the field. Analysis of the suitability of segregation ratio calculated with the chi squared formula and the degree of dominance could be seen from the comparison between the dominant predictive value [h] and the additive predictive value [d] were carried out with SAS 9.2 software. The results showed that the character of purple pigment was controlled by two mutually complementary dominant genes with recessive epistasis (9:3:4) which follow the model of additive×additive ([m][d][i]) and dominant×dominant ([m][d][l]) interaction. The action of black/purple pigment gene of rice was perfect dominance which was directed to the parent with purple pericarp pigment (black rice).

Keywords: pericarp pigment, inheritance, black rice, white rice

1. Introduction

Most of the rice consumed is white rice, although there are many cultivars of rice including those containing color pigments, such as red and black. The name of the rice is associated with the color/pigment (black, red or purple) formed by deposits of anthocyanin in the pericarp layer, seed coat (seed coat) or aleurone layer (Chaudhary, 2003). Colored rice has potential as a source of antioxidants and viable as a source of functional food (Yawadio *et al.*, 2007). Black rice has high anthocyanin content in the pericarp layer, which gives a dark purple pigment (Ryu *et al.*, 1998; Takashi *et al.*, 2001). Anthocyanins act as antioxidants that can clean up cholesterol in the blood, prevents anemia, potentially increasing the body's resistance to disease, improve liver cell

damage (hepatitis and cirrhosis), prevent impaired kidney function, prevent cancer/tumor, slow the aging (antiaging) (Harmanto, 2008), as well as to prevent narrowing of the arteries (atherosclerosis) and heart vessel disease (cardiovascular) (Ling *et al.*, 2001; Ling *et al.*, 2002). Black rice also contains protein, vitamins, and minerals higher than white rice (Suzuki *et al.*, 2004). Black rice is rich in the element iron (Fe), zinc (Zn), manganese (Mn) and phosphorus (P). The range of content of these elements is quite high depending on the variety, location and different soil types (Liu *et al.*, 1995; Qiu *et al.*, 1993; Zhang, 2000).

Local black rice has advantages, but also has drawbacks of perennial nature, tall plants, low production potential and unacceptable taste. Research towards the formation of black rice cultivars with superior properties of high productivity, early maturity, low plant habitus, high anthocyanin content and good taste in Indonesia is in slow progress. Research and inheritance of pigment pericarp of black rice abroad was conducted by Hsieh and Chang (1964); Mingwei *et al.* (1995); Sahu *et al.* (2011); Wang and Qingyao

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(2007) and Rahman *et al.* (2013). The pattern of inheritance of pigment rice with local black rice from Indonesia has not been known. Therefore, research towards the establishment of rice cultivars black rice superior needs to be done. This study was conducted to determine the pattern of inheritance of pigment in a cross between black rice of local Indonesian with white rice of superior variety.

2. Materials and Methods

Study of inheritance patterns of rice pigment using five population is parent P₁ = black rice of Magelang hairless (code S), Cempo ireng (code C) and parent P₂ = white rice of Situbagendit (code G) and Inpari 6 (code I), F₁ population (P₁ / P₂), F₂ (F₁ selfing) and F₃ (F₂ selfing). Evaluation of pericarp pigment of the rice is done on each individual rice plants. Rice pericarp pigment of each population morphology observed with partial peeling grains. Rice pigment observation based scoring colors as shown in Table 1.

Table 1. Score of pigment rice.

Trait	Score	Characteristic properties
Black	1	the percentage of black pigment in a single grain of rice ≥ 50 % ; referred to as Black = B
Medium black	2	the percentage of black pigment in a single grain of rice < 50 % ; referred to as Medium Black = MB
Red	3	the percentage of red pigment in a single grain of rice 100 % , referred to as Red = R
White	4	the percentage of white pigment in a single grain of rice 100 % , referred to as White = W

2.1 Data Analysis

2.1.1 Testing of rice pigment inheritance

The data observations of seed pericarp pigment based on the scoring yields from F₂ and F₃ generation populations of plants were analyzed using chi-square analysis (Singh and Chaudhary, 1979).

$$\chi^2 = \sum_{i=1}^n \frac{(O_i - E_i)^2}{E_i}$$

Description: O_i = number of phenotypes to i based on observations; E_i = the amount of the expected phenotype; n = the number of classes.

Value of χ^2 be compared with value table of χ^2 on appropriate degree of freedom. If the value of statistical χ^2 is smaller than the value of χ^2 , then the frequency distribution of F₂ population is in accordance with ratio expected.

2.1.2 Estimation of gene action and genetic parameters

- a. Homogeneity analysis of P₁, P₂ and F₁ population was Barlett test. Barlett test was conducted

in order to determine homogeneity of variance of population generations. Homogeneity analysis is done with the help of SAS V9.2 software.

- b. Determined the adequacy of additive-dominant model with Joint scaling test method (Mather and Jinks, 1982), with a prediction: Ho = follow the additive dominant model; Ha = not follow the additive-dominant model (following the epistasis model), if reject Ho, then considered to follow the epistasis model.

If following the additive-dominant model, then the estimate of the genetic component is done by the method of least weighted square method (w), with weights is an example and inverse variance (Rowe and Alexander, 1980), the genetic parameters are: [m], [d], and [h], with [m] = intercept, [d] = total effect of additive, and [h] = total effect of dominant.

If the additive-dominant models are not fulfilled, then the estimation of genetic parameters is done with six genetic parameters according to Mather and Jinks (1982), with the average population in five generations that is a combination of six genetic parameters, namely:

$$\begin{matrix} P1 \\ P2 \\ F1 \\ F2 \\ F3 \end{matrix} = \begin{pmatrix} 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & -1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 0,5 & 0 & 0 & 0,25 \\ 1 & 0 & 0,25 & 0 & 0 & 0,625 \end{pmatrix} \begin{pmatrix} m \\ d \\ h \\ i \\ j \\ l \end{pmatrix}$$

$$Y = C M$$

with [m] = intercept; [i] = additive-additive interaction; [d] = total effect of additive; [j] = interaction of additive-dominant and dominant-additive; [h] = total effect of dominant; [l] = dominant-dominant interaction; Y = average of generation; C = genetic model that depend on a M parameter which will allegedly; M = genetic parameters were estimated by the least squares consisting of [m], [d], [h], [i] [j], and [l].

Estimation analysis of genetic parameter was performed using SAS V.9.2 software with Proc. GLM on scoring pigment data from generation population of P₁, P₂, F₁, F₂ and F₃.

2.1.3 The degree of dominance

The degree of dominance can be seen from the comparison between the dominant predictive value [h] with the additive predictive value [d] (Mather & Jinks, 1982). Criteria for the degree of dominance by Petr and Frey (1966) that if the value of the degree of dominance in the range of 0 and 1 indicates the trait is controlled by a dominant gene is not perfect, if the value of the degree of dominance in the range of -1 and 0 indicating the trait is controlled by a negative dominant gene with not perfect. If the value of the degree of dominance = 0 then the character is no dominance, if the degree of dominance is worth 1 or -1 indicates the character is a dominance gene controlled perfectly and if the degree of dominance is less than -1 or more than 1 indicate the character is a controlled by gene action of over dominance.

3. Results and Discussion

3.1 Testing of rice pigment inheritance

Testing of the rice pigment and pattern of inheritance of genetic parameters testing performed on three cross combinations between black rice with white rice: black rice of Magelang hairless (S/black) × Situbagendit (G/white); Cempo ireng (C/black) × Situbagendit (G/white) and Cempo ireng (C/black) × Inpari 6 (I/white). Rice pigment inheritance estimated using P₁, P₂, F₁, F₂ and F₃ population

In Table 2 it appears that the diversity of score pigment two parents (P₁ and P₂) and the third cross F₁ (S × G; C × G, and C × I) was not significantly (Pr = 0.4579; Pr = 0.9404; Pr = 0.9981). This shows the third population is homogenous population with a mean different. The mean pigment score of F₁ (pigment score = 1.0254 and 1.0412) is similar to the black rice of S and C cultivar as P₁ parent (pigment score = of 1.0462 and 1.0500) lower than the mean scores of white rice of G and I cultivar as P₂ parents (pigment score of 4.0346 and 4.0462). This means of the two parents pigment, based on different pigment score with value of low score pigment was dominant than value of high pigment score. F₂ plants will be segregate shown by value of variance greater than the value of the two parents and F₁ (Bartlett test Pr = 0.0001; Table 2).

The observation of the pigment of F₂ rice plant population (630 individual plants of S×G, 920 individual plants of C×G and 472 individual plants of C×I) and the plant population F₃ (3,527 individual plants of S×G, 3942 individual plants of C×G and 2,588 individual plants of C×I) were grouped into four groups, namely: Black (B); Medium Black (MB); Red (R) and White (W) (Table 3).

Using one locus model, segregation in F₂ and F₃ showed that ¾ of the population was black rice (black and

medium black) and the remaining ¼ of the population was not black rice (red and white). Results sorting of one locus model with 3:1 ratio in the F₂ and F₃ populations of S×G; C×G and C×I crossing can be accepted at the level of 0.05 (Table 3, except F₃ C×G and C×I). These results are consistent with Rahman *et al* (2013) that the cross of Kewha black rice and Kumpangbyeo white rice provide segregation in F₂ and F₃ generation with ratio of 3 black: 1 white so black pigment dominant over white pericarp.

Crosses using two different parents with F₁ is similar to one of the parents may also occur under two loci model with two alleles per locus and the results of chi-square analysis (S×G, C×G and C×I crossing) showed irregularities ratio of 9:3:3:1 both in F₂ and F₃ populations (Table 3). Therefore, the analysis continued by sorting into two groups and three groups. The analysis of F₂ population that is linear with F₃ population is the sorting of three groups: 9:3:4 or recessive epistasis on S×G, C×G, and C×I crossing (Table 3). Recessive epistasis occurs when the recessive allele in a gene cover or reduce the expression phenotypes alleles in other genes. This is in accordance with Acquah (2007) and Hartl (2009), that the cross using two different parents with F₁ is similar to one of the parents may also occur under two loci model with two alleles per locus for the gene action was complements with 9: 7 ratio; or duplicate genes with ratio 15:1; or additive genes with a ratio of 9:6:1; or dominant epistasis with a ratio of 12:3:1; or recessive epistasis with a ratio of 9:3:4; or suppression dominant with the ratio 13:3.

3.2 Estimation of gene action and genetic parameters

Analysis of the average generation using P₁, P₂, F₁, F₂ and F₃ generation populations are conducted to determine the behavior of the rice pigment. Results of the average generation analysis at S×G; C×G and C×I crossing showed

Table 2. The mean and variance of scores pigment in populations P₁, P₂, F₁ and F₂ on S×G; C×G and C×I crossing.

Generation	Crossing		
	S × G	C × G	C × I
P ₁ \bar{X}	1.0460	1.0500	1.0462
σ^2	0.0066	0.0058	0.0066
P ₂ \bar{X}	4.0340	4.0462	4.0462
σ^2	0.0056	0.0066	0.0066
F ₁ \bar{X}	1.0254	1.0412	1.0412
σ^2	0.0043	0.0065	0.0065
F ₂ \bar{X}	1.7809	1.9772	1.9788
σ^2	1.1379	1.5914	1.5749
F ₃ \bar{X}	1.7116	2.1110	1.5858
σ^2	0.9682	1.9618	0.9826
Mean and variance test			
Ho	Pr		
$\mu_{P1} = \mu_{P2} = \mu_{F1}$	< 0.0001	< 0.0001	< 0.0001
$\mu_{P1} = \mu_{P2}$	< 0.0001	< 0.0001	< 0.0001
$\mu_{F1} = \mu_{P1}$	0.2373	0.6464	0.7987
$\mu_{F1} = \mu_{P2}$	< 0.0001	< 0.0001	< 0.0001
$\mu_{F1} = \mu_{MP}$	< 0.0001	< 0.0001	< 0.0001
$\sigma^2_{P1} = \sigma^2_{P2} = \sigma^2_{F1}$	0.4579	0.9404	0.9981
σ^2_{F2}	0.0001	0.0001	0.0001

Table 3. Results of chi-squared analysis of F₂ and F₃ populations at SxG; CxG and CxI crossing.

Crossing	F ₂ Generation		F ₃ Generation	
	Observed	χ^2	Observed	χ^2
S x G	B = 365	Monogenic	B = 2140	Monogenic
	MB = 95	3 : 1 (1.43 ^{ns})	MB = 489	3 : 1 (0.424 ^{ns})
	R = 103	Digenic	R = 676	Digenic
	W = 67	9:3:3:1 (26.16 [*])	W = 222	9:3:3:1 (57.51 [*])
	Σ = 630	9 : 7 (2.878 ^{ns})	Σ = 3527	12:3:1 (1.343 ^{ns})
	13:3 (2.229 ^{ns})		9:6:1 (3.033 ^{ns})	
	9:3:4 (5.838 ^{ns})		9:3:4 (3.092 ^{ns})	
			13:3 (0.429 ^{ns})	
			15:1 (0.005 ^{ns})	
C x G	B = 503MB	Monogenic	B = 2304	Monogenic
	MB = 174	3 : 1 (1.057 ^{ns})	MB = 966	3 : 1 (132.54 [*])
	R = 4	Digenic	R = 6	Digenic
	W = 239	9:3:3:1 (737.92 [*])	W = 666	9:3:3:1 (1514.9 [*])
	Σ = 920	9 : 7 (0.866 ^{ns})	Σ = 3942	9:6:1 (1.600 ^{ns})
	9:3:4 (1.154 ^{ns})		9:3:4 (2.972 ^{ns})	
C x I	B = 256	Monogenic	B = 1716	Monogenic
	MB = 90	3 : 1 (0.816 ^{ns})	MB = 543	3 : 1 (207.7 [*])
	R = 6	Digenic	R = 14	Digenic
	W = 120	9:3:3:1 (354.91 [*])	W = 315	9:3:3:1 (656.3 [*])
	Σ = 472	9 : 7 (0.697 ^{ns})	Σ = 2588	9 : 7 (2.299 ^{ns})
	9:3:4 (0.907 ^{ns})		9:3:4 (3.194 ^{ns})	

Note: * = significant at $\alpha = 5\%$, meaning that the ratio of hope was rejected, ns = not significant at $\alpha = 5\%$, meaning that the ratio of hope received; B = Black; MB = Medium Black; R = Red; and W = White.

that the behavior of rice pigment characters can be explained by using additive-dominance model. However, the gene action of additive-dominance at two loci with two alleles per locus model both in F₂ and F₃ population are deviate from 9:3:3:1 ratio (Table 3). Therefore, the test continued to interactions locus (epistasis) for black color rice character using mean analysis generation. Results of mean analysis generation at SxG; CxG and CxI crossing showed that the behavior of pigment rice can be explained using additive-dominant model with additives-additives and dominant-dominant interaction with three genetic component, m [d] [i] and m [d] [l] (Table 4). Singh and Chaudhary (1979) states that the role of these genetic components can be tested by comparing t statistical with t table as on the individual scale test. The value of additive genetic components and additive-additive and dominant-dominant interaction is significant at 5% and 10% level.

Value of dominant genetic component [h] and dominant \times dominant [l] interaction have the same sign (ie negative). This suggests a recessive epistasis gene action in accordance with the results of chi-square analysis with a ratio of 9:3:4 (recessive epistasis) in the F₂ and F₃ generation (Table 3). Mather and Jinks (1982), said that when the dominant genetic component [h] and the dominant \times dominant interaction has a value with the same sign then indicates a complementary gene action or recessive epistasis. Negative values at the genetic component dominance [h] and the interaction of dominant \times dominant [l] (Table 4) shows that these components tend to be more directed to parent who have on average lower, in this case leads to the parent by black pigment rice (score of black pigment rice = 1, the pigment of the lowest scores). In accordance with Arif *et al.* (2012), if component dominant \times dominant genetic parameter is

negative, then the components are more likely to lead to parent who have an average value lower.

Results of chi-squared analysis on F₂ and F₃ populations and based on the analysis of the mean generation that inheritance of rice pigment character (black) at SxG; CxG and CxI crossing is controlled by two pairs of genes to influence recessive epistasis ratio of 9:3:4, with photos chronologically from crosses presented in Appendix Figure 1 (SxG crossing), Figure 2 (CxG crossing) and Figure 3 (CxI crossing).

Grouping pigment in chi-square analysis in 9: 3: 4 ratio (9B: 3 MB: 4 instead of black), with pigment instead of black consists of two groups of pigments are brown rice and white rice. This is due to a recessive epistasis effect on anthocyanin biosynthesis process. Allegedly, during the process of anthocyanin biosynthesis inhibition encoding the enzyme chalcone Synthase (CHS), or overexpression (over encoding) of dihydroflavonol reductase gene (DHFR) on a portion of the plant so that the recessive allele at the gene expression phenotypes cover or reduce the alleles in second genes. According Gutterson (1995) and Tanaka *et al.* (1998), with the approach of inhibition (silencing) and excess encoding gene (overexpression) in the phenylpropanoid pathway that produces anthocyanins can be done to produce the flower color on purpose, as stated by Gutterson *et al.* (1994) on the formation of white chrysanthemums done by inhibiting the gene encoding chalcone syntase (CHS) and Tanaka *et al.* (1995) on the formation of the red-brick petunia flowers by enhancing the encoding (overexpression) of dihydroflavonol reductase gene (DHFR).

Based on the above results, *Pb* and *Pp* genes were dominant to encourage the formation of anthocyanin expressed as black of rice, while *pb* and *pp* genes in homozygous state inhibit the formation of anthocyanins so that

Table 4. Test the suitability of additive-dominant model of S×G; C×G and C×I crossing for black pigment rice.

	Crossing of S × G	Crossing of C × G	Crossing of C × I
β	Predictive value	Predictive value	Predictive value
m	2.428 ± 0.166**	2.54 ± 0.037**	2.43 ± 0.202**
[d]	-1.504 ± 0.185**	-1.498 ± 0.039**	-1.500 ± 0.22**
[h]	-1.429 ± 0.236**	-1.499 ± 0.056**	-1.424 ± 0.306**
F stat	54.28 **	1031.3 **	34.08 **
R ² (%)	98.19	99.90	97.15
m	1.208 ± 0.217**	1.298 ± 0.318*	1.199 ± 0.189**
[d]	-1.494 ± 0.297**	-1.498 ± 0.355*	-1.500 ± 0.211**
[i]	1.332 ± 0.367*	1.249 ± 0.476*	1.346 ± 0.291**
F stat	20.73 **	11.85*	33.71**
R ² (%)	95.40	92.22	97.12
m	2.320 ± 0.245**	2.479 ± 0.099**	2.366 ± 0.271**
[d]	-1.513 ± 0.291**	-1.494 ± 0.110**	-1.500 ± 0.311**
[l]	-1.307 ± 0.354*	-1.444 ± 0.153*	-1.309 ± 0.417*
F stat	21.39 **	130.49 **	16.56 **
R ² (%)	95.53	99.22	94.30

Note: * = significant α = 5 %; ** = significant α = 10 %; β = genetic parameter estimators; [m] = intercept = mean generation effect; [d] = additive effect; [h]= dominant effect; [i] = additive - additive interaction; [l] = dominant-dominant interaction; R²= coefficient of determination.

white of rice. Based on the possibility of S×G; C×G, and C×I crossing in Figure 1, *Pb* genes responsible for the distribution/spread of anthocyanin and *Pp* genes controlling of anthocyanin synthesis. Individual plants having *Pb-Pp* genotype to produce of large anthocyanins was expressed as black rice pericarp. Plants with *pbpbPp-* genotype to produce of low anthocyanins number because it has a *pbpb* genotype was expressed as medium black the pericarp. Furthermore, plants with red and white pericarp not produce anthocyanins (no purple) because the plant has *pppp* recessive gene. Wang and Qingyao (2007) and Wang et al. (2009) say that the *Pb* genes responsible for the accumulation of brown pericarp pigment and black rice pericarp requires *Pp* gene.

Research results of Rahman *et al.* (2013), at crossing of black rice 'Heugnamybeo' (*PbPbPpPp*) with three varieties of white rice 'Hwayongbyeo', 'Ishikari' and 'Ipombyeo' (*pbpbpppp*) give segregation in the ratio 9 black: 3 brown: 4 white; sianidin -3-O-glycoside content higher in black seeds / dark purple (*Pb-PpPp*) of the medium black / medium purple pigment (*Pb-Pppp*). Seeds with red pericarp (*Pb-pppp*) or white pericarp (*pbpbpppp*) are an expression of the absence sianidin-3-O-glucoside. These results indicate that the level of sianidin-3-O-glucoside, which is one type of anthocyanins which are contained in black rice, is determined by the copy number of *Pp* alleles.

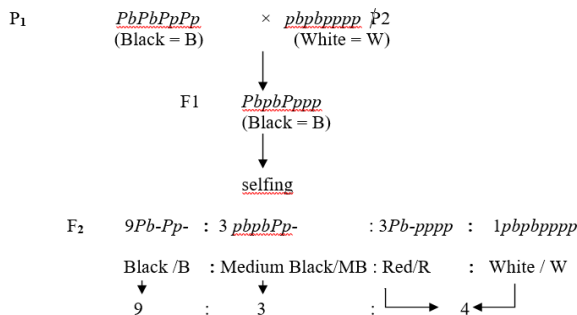


Figure 1. Possibility of black rice and white rice crossing.

4. Conclusions

The character of purple pigment at the crossing between black and white rice was controlled by two mutually complementary dominant genes with recessive epistasis (ratio 9:3:4) which follow the model of additive×additive ([m][d][i] and dominant×dominant ([m][d][l]) interaction. The action of the gene for the black pigment of rice was perfect dominance which was directed to the parent with purple pericarp pigment (black rice).

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