Genetic analysis on grain physical characteristics and grain color from the crosses of black × white rice genotypes

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Abstract. *Nurhidayah S, Firmansyah E, Haryanto TAD, Dewi PS. 2021. Genetic studies of grain physical characteristics and grain color from the crosses of black × white rice genotypes. Biodiversitas 22: 2763-2772.* This study was conducted to investigate genetic variance, cytoplasmic maternal effect, gene action, and broad-sense heritability of grain physical characteristics and grain color from crosses of black × white rice genotypes (*Oryza sativa*). Genetic studies were conducted using F2 generations from the crosses of black × white rice genotypes and their reciprocal crosses. The plant materials consisted of seven black rice genotypes (PH2, PH3, PH4, PH5, PH6, PH7, and PH8), three commercial white rice varieties (Inpari 13, Inpari 18, and Inpari 19), a total of 30 F2 generations, and their reciprocal crosses. There are four-grain physical traits examined: grain length, grain width, grain thickness, and grain color. The result showed that maternal cytoplasmic effect was present in most F2 generations and their reciprocal crosses. The characters of grain length, grain width, and grain thickness are controlled by polygene with additive action. Based on the results of the Chi-Square Test, the grain color did not follow the expected 1: 2: 1 ratio for incomplete dominance involving monogenic traits. Broad sense heritability for grain length, grain width, and grain thickness are varied from low to medium for a cross of black rice genotypes × Inpari 19, and low to high for the crosses of black rice genotypes × Inpari 13 and black rice genotypes × Inpari 18.

Keywords: Gene action, heritability, kurtosis, maternal cytoplasmic, skewness

INTRODUCTION

Oryza sativa (a monocotyledonous grasses) is the most widely rice species grown worldwide including in Asia, North and South American, European Union, Middle Eastern, and African countries. *O. glaberrima*, however, is grown solely in West African countries. Black rice is a type of the rice species *O. Sativa*. It is also known as purple rice, forbidden rice, heaven rice, imperial rice, king's rice and prized rice. Many people assume this rice as a panacea of many culinary diseases because of its high nutritive value and curative effect. There are more than 200 types of black rice varieties in the world. Only China is dominant producer of black rice with 62% of total global production sharing. Moreover, China has successfully developed more than 54 modern black rice varieties with high yield characteristics and multiple resistances, followed by Sri Lanka, Indonesia, India and Philippines (Kushwaha 2016). In Indonesia, there are many names of local pigmented rice landrace in many regions included Cempo Ireng, Jawa Melik, Melik, Hitam Toraja, Hitam Kalimantan, and Hitam Lampung (Kurniasih et al. 2019).

Black rice is a functional food in Indonesia. It is defined as foods that promote health by reducing the disease risk and slowing the aging process and enhancing the immune response. It has many phytochemical contains including anthocyanin, oryzanol, etc. (Pratiwi and Purwestri 2017). Black rice contains a higher level of anthocyanin which has higher antioxidant activity than white rice. Pigmentation in black rice results from the activity of the *Kala4* gene, which is necessary for anthocyanin synthesis. This same study suggested that mutations in the promoter of *Kala*4 give rise to the black rice phenotype. This mutation arose in tropical *japonica* and then spread to the *indica* subspecies subsequently (Oikawa et al. 2015). According to Carsono et al. (2014), the quality of rice is very important in the rice marketing strategy both on a domestic and international scale.

Wolf and Wade (2009) distinguish maternal cytoplasmic inheritance to specifically referring to organelle inheritance via the egg. In most cases of uniparental inheritance, the offspring are genetically identical (other than new variation caused by mutation) to their mothers for their cytoplasmic genotype. When the maternal genotype and phenotype have no causal influence on the offspring phenotype, this case is not a maternal effect. The degradation of cytoplasmic DNAs in male reproductive cells occurs in many angiosperms that display maternal cytoplasmic inheritance. There is a positives relationship between the male cytoplasmic DNA degradation during pollen development and the presence of nucleases with high activity in pollen or stamen. In plants displaying maternal inheritance, degradation of cytoplasmic DNAs occurs during the development of male reproductive cell, and the nucleolytic activities were detected in the pollen or stamen proteins (Li and Sodmergen 1995). Several crosses have been made from black × white rice genotypes and their reciprocal crosses.

The black rice genotypes were collected from Tasikmalaya, West Java and the white rice genotypes are the commercial white rice varieties. Aims of this study were: (i) to identify grain physical characters from F2 generations and their reciprocal crosses, (ii) to estimate the components of genetic variance and the heritability of important quantitative rice grain traits, (iii) to determine gene action and maternal cytoplasmic effect, and (iv) to observe the phenotypic ratios of grain color in the F2 generations and their reciprocal crosses.

MATERIALS AND METHODS

Plant material

The experiments were carried out at the Perjuangan University of Tasikmalaya, West Java, Indonesia started from September to November 2020. This study used seven genotypes of black rice (PH2, PH3, PH4, PH5, PH6, PH7, PH8) from the germplasm collections of the Perjuangan University of Tasikmalaya (Nurhidayah and Umbara 2019), and three commercial varieties of rice (Inpari 13, Inpari 18, and Inpari 19) provided by Indonesia Center for Rice Research (ICRR) Subang Regency, West Java. The parental genotypes with their reciprocal crosses were used to produce F1 offsprings and their reciprocal crosses. These offsprings resulted in 30 F2 generations and their reciprocal ones (Table 1). Each crossing consisted of 193–300 grains.

Data collection

Fully filled grains were prepared for measuring grain length, grain width, and grain thickness as followed (Figure 1). This measurement was calculated based on 250-300 grains per genotype. Grain length was measured as the distance from the base of the lowermost glume to the tip (apiculus) of the fertile lemma or palea, whichever is longer using the vernier caliper. Grain width was measured as the distance across the fertile lemma and palea at the widest point with the vernier caliper. Measurement of seed thickness is taken at the position of the largest seeds then measured using a vernier caliper. Color measurement used guidelines from Descriptors for Wild and Cultivated Rice (*Oryza* spp.) from the International Rice Research Institute/IRRI (Biodiversity International 2007).

Data analysis

Each data collection was analyzed using STAR 2.0.1 application. Estimation of gene action and the number of genes controlling the trait at each cross were analyzed using the F2 data distribution from the skewness and kurtosis values. Estimation of maternal effects used Student's t-test to see whether there were differences in the female parents used in each set of crosses. Data of character results were analyzed using Mahmud Kramer-Method to search for variance components (genetic variance, environmental variance, phenotype variance), and heritability. The calculation of the variance component is as follows:

$$\sigma^2_{F2} = \sigma^2_P$$
$$\sigma^2_E = \sqrt{\sigma^2_{P1} \sigma^2_{P2}}$$
$$\sigma^2_G = \sigma^2_P - \sigma^2_E$$
$$h^2 = \frac{\sigma 2F2 - \sqrt{\sigma 2P1 \sigma 2P2}}{\sigma 2F2} \times 100\%$$
$$CVG = \frac{\sqrt{\sigma 2G}}{\bar{x}}$$

Note: σ^2_P: phenotype variance, σ^2_E: environmental variance, σ^2_G: genetic variance, h^2_{ns}: broad-sense heritability

Table 1. F2 generations from the crosses of black × white rice genotypes and their reciprocal crosses.

| F2 generation	F2 generation	F2 generation
PH2×Inpari 13	PH3× Inpari 18	PH3× Inpari 19
Inpari 13×PH2	Inpari 18×PH3	Inpari 19×PH3
PH3× Inpari 13	PH4× Inpari 18	PH5× Inpari 19
Inpari 13×PH3	Inpari 18×PH4	Inpari 19×PH5
PH4× Inpari 13	PH5× Inpari 18	PH6× Inpari 19
Inpari 13×PH4	Inpari 18×PH5	Inpari 19×PH6
PH5× Inpari 13	PH8× Inpari 18	PH7× Inpari 19
Inpari 13×PH5	Inpari 18×PH8	Inpari 19×PH7
PH8× Inpari 13	PH2× Inpari 19	PH8× Inpari 19
Inpari 13×PH8	Inpari 19×PH2	Inpari 19×PH8
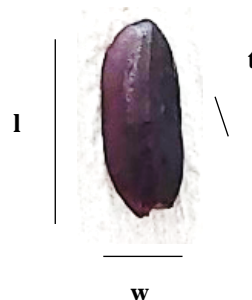
Figure 1. Measrment of data collection. Note: l: length, w: width, and t: thickness

RESULTS AND DISCUSSION

Performance of grain physical characteristics and maternal cytoplasmic effects on F2 crosses and their reciprocal ones

Rice grain quality is a complex trait that reflects producers, processors, sellers, and consumers' opinions regarding production, processing, marketing, and consumption of the grain (Zhou et al. 2019; Xiong et al. 2020). According to Huang et al. (2017), grain size (length, width, and thickness) and shape are crucial for grain yield and grain appearance in crops, and Zhao et al. (2018), it is one of the key determinants of both yield and quality of rice. Based on Table 2, the mean value of each cross shows different performances. When F2 generations resulted from crosses between black rice genotypes as the pistil parent and white rice varieties as the pollen parent, there was variation of grain length compared to their F2 reciprocal

crosses. From the results of the t-test, the black rice genotypes had significantly shorter grain length (5.87-6.49 mm) than that of white rice (Inpari13 variety) (6.55 mm), except for the cross of PH4×Inpari 13 and its reciprocal of Inpari 13×PH4 that showed no difference.

When black rice genotypes were crossed with white rice variety of Inpari 18, all combinations of crosses and their reciprocal crosses show the difference between both parents. Inpari 18 has longer grain length compared to black rice genotypes, which is around 6.95 mm, while black rice is around 5.87-6.49 mm. The crosses between black rice genotypes with Inpari 19 and their reciprocal crosses, also showed differences. Inpari 19 rice has grain length of 6.77 mm, significantly longer than the black rice genotypes except for the cross of PH2×Inpari 19 and its reciprocal cross.

The effect of female parents at each cross shows a variation in the grain length of the F2 population (Figure 2 and Table 2). This can be seen from the t-test between F2 and F2 reciprocal crosses. All F2 generations show different performances when using female parents of black rice crossed with male parents of white rice and their

reciprocal crosses. Maternal effect applied for almost all cross combinations of black rice × white rice genotypes and their reciprocal crosses except for the cross combinations of PH3×Inpari 19 and PH7×Inpari 19. Razzaque et al. (2019) reported a strong maternal cytoplasmic effect in controlling rice plants due to salinity stress.

Based on the t-test in Table 3, the crosses of black rice × white rice genotypes and their reciprocal crosses indicated differences in the grain width. Black rice genotypes have higher grain width than white rice varieties of Inpari 13, Inpari 18 and Inpari 19. The F2 generations from the crosses of black rice × white rice genotypes and their reciprocal crosses were below the mean of both parents except for 6 cross combinations which have the mean between both parents, namely PH2×Inpari 13 (Figure 3), Inpari 13×PH2, PH3× Inpari 13, Inpari 13×PH4, PH5× Inpari 19, and Inpari 19×PH6. Although the mean of the F2 generations tends to be shorter than those of their parents, some F2 individuals are having higher grain width than those of their parents, which spread over 15 cross combinations.

Table 2. Genetic variance of grain length of the parental genotypes, F2 generations of black × white rice genotypes and their reciprocal crosses

Cross combination (pistil parent × pollen parent)	Pistil parent	Pollen parent	t-value	Mean of F2	t-value F2 – F2R	Range population of F2 generation (min-max)
PH2×Inpari 13	6.06±0.33	6.55±0.43	-13.88*	6.26±0.45	2.90*	4.30–7.50
Inpari 13×PH2	6.55±0.43	6.06±0.33	13.88*	6.15±0.32		5.08–6.87
PH3× Inpari 13	5.87±0.33	6.55±0.43	-20.59*	6.22±0.44	-2.44*	5.00–7.10
Inpari 13×PH3	6.55±0.43	5.87±0.33	20.59*	6.34±0.34		5.42–7.22
PH4× Inpari 13	6.40±0.43	6.55±0.43	-0.89ns	6.42±0.41	-4.19*	4.80–7.40
Inpari 13×PH4	6.55±0.43	6.49±0.43	0.89ns	6.56±0.40		3.05–8.17
PH5× Inpari 13	6.10±0.47	6.55±0.43	-10.15*	6.39±0.44	-3.32*	4.90–7.40
Inpari 13×PH5	6.55±0.43	6.10±0.47	10.15*	6.45±0.35		5.33–7.28
PH8× Inpari 13	5.89±0.39	6.55±0.43	-16.79*	6.45±0.37	2.93*	5.30–7.50
Inpari 13×PH8	6.55±0.43	5.89±0.39	16.79*	6.36±0.36		5.00–6.26
PH3× Inpari 18	5.87±0.33	6.95±0.29	-28.66*	6.97±0.39	7.29*	5.70–7.90
Inpari 18×PH3	6.95±0.29	5.87±0.33	28.66*	6.71±0.46		2.26–9.78
PH4× Inpari 18	6.49±0.43	6.95±0.29	-10.81*	6.89±0.45	-3.70*	5.40–7.90
Inpari 18×PH4	6.95±0.29	6.49±0.43	10.81*	7.01±0.37		5.80–7.91
PH5× Inpari 18	6.10±0.47	6.95±0.29	-19.47*	6.75±0.71	5.56*	5.00–7.90
Inpari 18×PH5	6.95±0.29	6.10±0.47	19.47*	6.44±0.40		5.29–8.32
PH8× Inpari 18	5.89±0.39	6.95±0.29	-26.33*	6.31±0.44	-16.40*	4.50–7.50
Inpari 18×PH8	6.95±0.29	5.89±0.39	26.33*	6.91±0.35		5.74–7.90
PH2× Inpari 19	6.06±0.33	6.77±0.37	-1.09ns	6.51±0.32	4.24*	5.00–7.70
Inpari 19×PH2	6.77±0.37	6.06±0.33	1.09ns	6.42±0.29		5.51–7.04
PH3× Inpari 19	5.87±0.33	6.77±0.37	-31.76*	6.46±0.38	1.44ns	4.50–7.30
Inpari 19×PH3	6.77±0.37	5.87±0.33	31.76*	6.41±0.31		5.52–7.23
PH5× Inpari 19	6.10±0.47	6.77±0.37	-19.83*	6.96±0.40	8.71*	5.90–8.00
Inpari 19×PH5	6.77±0.37	6.10±0.47	19.83*	6.69±0.38		5.42–7.62
PH6× Inpari 19	6.52±0.40	6.77±0.37	-8.30*	6.86±0.36	1.59ns	5.30–7.70
Inpari 19×PH6	6.77±0.37	6.52±0.40	8.30*	6.80±0.29		5.50–7.50
PH7× Inpari 19	5.88±0.46	6.77±0.37	-26.03*	6.48±0.35	1.66ns	5.20–7.50
Inpari 19×PH7	6.77±0.37	5.88±0.46	26.03*	6.42±0.39		4.90–7.30
PH8× Inpari 19	5.89±0.39	6.77±0.37	-27.88*	6.64±0.35	-2.31*	5.60–8.60
Inpari 19×PH8	6.77±0.37	5.89±0.39	27.88*	6.71±0.40		5.10–7.50

Note: F2: Filial 2, F2R: Reciprocal cross of F2, *: significant at level of 0.05; ns: not significant at level 0.05

Table 3. Genetic variability analysis for grain width of rice in parental and F2 generation

Cross combination (pistil parent × pollen parent)	Pistil parent	Pollen parent	t-value	Mean of F2	t-value F2 – F2R	Range population of F2 generation (min-max)
PH2×Inpari 13	2.51±0.11	2.28 ± 0.12	23.57*	1.80±0.24	-24.32*	1.20–2.50
Inpari 13×PH2	2.28±0.12	2.51 ± 0.11	-23.57*	2.21±0.10		1.52–2.43
PH3× Inpari 13	2.47±0.17	2.28 ± 0.12	21.21*	2.27±0.15	2.34*	1.70–2.80
Inpari 13×PH3	2.28±0.12	2.47 ± 0.17	-21.21*	2.25±0.12		1.28–2.88
PH4× Inpari 13	2.65±0.15	2.28 ± 0.12	35.83*	1.82±0.19	-40.59*	1.00–2.20
Inpari 13×PH4	2.28±0.12	2.65 ± 0.15	-35.83*	2.35±0.10		1.74–2.68
PH5× Inpari 13	2.50±0.14	2.28 ± 0.12	22.11*	1.63±0.26	-40.46*	0.90–2.10
Inpari 13×PH5	2.28±0.12	2.50 ± 0.14	-22.11*	2.27±0.15		1.67–2.78
PH8× Inpari 13	2.47±0.14	2.28 ± 0.12	17.47*	1.84±0.16	-21.13*	1.20–2.20
Inpari 13×PH8	2.28±0.12	2.47 ± 0.14	-17.47*	2.06±0.09		1.69–2.66
PH3× Inpari 18	2.47±0.17	2.41 ± 0.13	6.95*	1.86±0.22	-31.32*	1.20–2.40
Inpari 18×PH3	2.41±0.13	2.47 ± 0.17	-6.95*	2.32±0.11		1.90–2.66
PH4× Inpari 18	2.65±0.15	2.41 ± 0.13	21.58*	1.90±0.21	-26.95*	1.30–2.80
Inpari 18×PH4	2.41±0.13	2.65 ± 0.15	-21.58*	2.31±0.11		1.80-2.81
PH5× Inpari 18	2.50±0.14	2.41 ± 0.13	9.42*	1.90±0.23	-21.07*	1.00–2.52
Inpari 18×PH5	2.41±0.13	2.50 ± 0.14	-9.42*	2.27±0.15		1.70–2.54
PH8× Inpari 18	2.47±0.14	2.41 ± 0.13	7.01*	1.83±0.23	-29.64*	1.00–2.30
Inpari 18×PH8	2.41±0.13	2.47 ± 0.14	-7.01*	2.30±0.09		1.85–2.77
PH2× Inpari 19	2.51±0.11	2.29 ± 0.11	24.54*	2.27±0.10	6.75*	2.00–2.50
Inpari 19×PH2	2.29±0.11	2.51 ± 0.11	-24.54*	2.21±0.14		1.55–2.47
PH3× Inpari 19	2.47±0.17	2.29 ± 0.11	18.07*	2.26±0.09	3.66*	2.00–2.50
Inpari 19×PH3	2.29±0.11	2.47 ± 0.17	-18.07*	2.22±0.12		1.73–2.90
PH5× Inpari 19	2.50±0.14	2.29 ± 0.11	20.09*	2.32±0.09	7.84*	2.10–2.50
Inpari 19×PH5	2.29±0.11	2.50 ± 0.14	-20.09*	2.23±0.13		1.93–2.59
PH6× Inpari 19	2.65±0.13	2.29 ± 0.11	35.06*	2.28±0.11	-12.79*	1.90–2.50
Inpari 19×PH6	2.29±0.11	2.65 ± 0.13	-35.06*	2.39±0.10		2.00–2.60
PH7× Inpari 19	2.49±0.15	2.29 ± 0.11	18.80*	2.24±0.10	39.20*	1.70–2.40
Inpari 19×PH7	2.29±0.11	2.49 ± 0.15	-18.80*	1.71±0.20		1.20–2.30
PH8× Inpari 19	2.47±0.14	2.29 ± 0.11	17.35*	2.30±0.09	2.97*	1.90–2.50
Inpari 19×PH8	2.29±0.11	2.47 ± 0.14	-17.35*	2.27±0.12		1.90–2.50

Note: F2: Filial 2, F2R: Reciprocal cross of F2, *: significant at level of 0.05; ns: not significant at level 0.05

From all cross combinations, it appears that there is a maternal effect on each combination of the crosses. This can be seen from the results of the t-test at each cross. F2 generations with pistil parents of white rice varieties showed higher average width grain than pistil parents of black rice genotypes (Figure 2). The effect of the maternal effect is also found in the oil content which accounts for 75% of *Brassica napus* (Guo et al. 2017). In contrast, the crosses between black rice genotypes and white rice variety of Inpari 19, showed higher grain width than their reciprocal crosses, except the PH6×Inpari 19 cross. Guo et al. (2017) stated that reciprocal crosses on rapeseed showed varied results which demonstrated that the environment might influence maternal cytoplasmic effect.

Based on Table 4, grain thickness in each cross combination shows different values. The black rice genotypes tend to be thinner compared to the white rice varieties. The black rice genotypes were around 1.57-1.71 mm thick, while the white rice varieties of Inpari 13, Inpari 18 and Inpari 19 were 1.86 mm, 184 mm, and 1.80 mm, respectively. The t-test also supports this that both parents have different grain thicknesses.

Indrasari et al. (2016) reported that 53% of respondents chose rice according to the grain shape. In Table 4 and Figure 4, the F2 generation of each cross has a different mean. In general, the F2 generation originated from pistil parents of black rice genotypes tend to have thinner grain shapes than pollen parents. A total of 12 cross combinations had thicker grain shapes if the pistil parents used white rice varieties, except for the other three combinations with different values. The range of F2 values varies from those below the parent to the range of the two parents. Almost all F2 generations show thicker grain rice than their parents, except for two crosses with maximum value below their parents. Based on the oil content differences between the reciprocal crosses in rapeseeds, there was a significant cytoplasmic effect on oil content (Wang et al. 2010). El-Bok et al. (2013) stated that plant improvement by utilizing the cytoplasmic effect is useful in increasing the protein content of wheat. Zangi et al. (2010) reported the existence of a maternal cytoplasmic effect on cotton crosses. Tao et al. (2011) detected cytoplasmic variation significantly affected grain weight in indica rice across the two experimental locations.
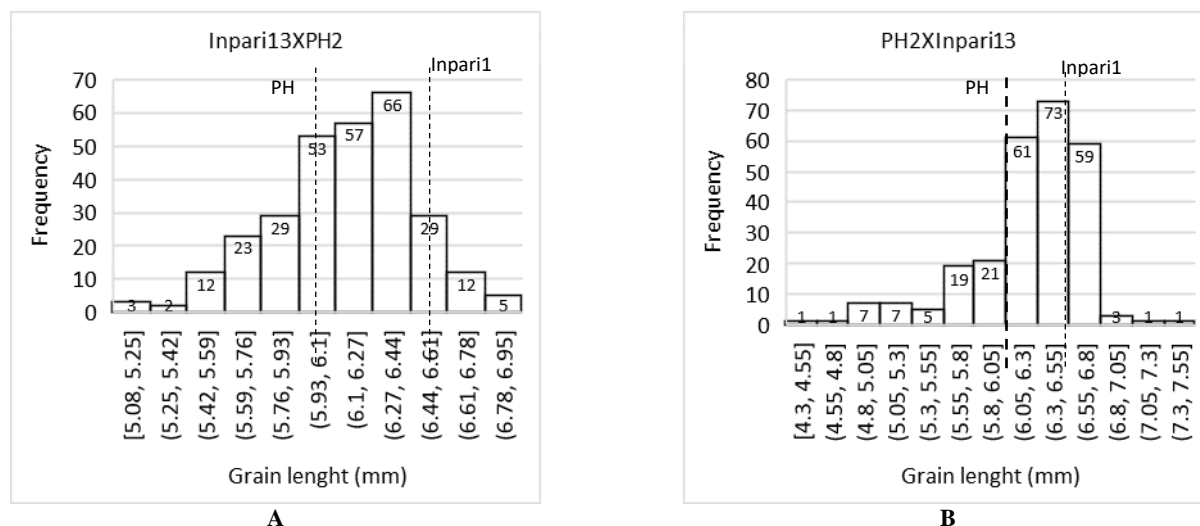
Figure 2. Variation of grain length from the F2 population of PH2 × Inpari 13 (A) and its reciprocal cross (B)
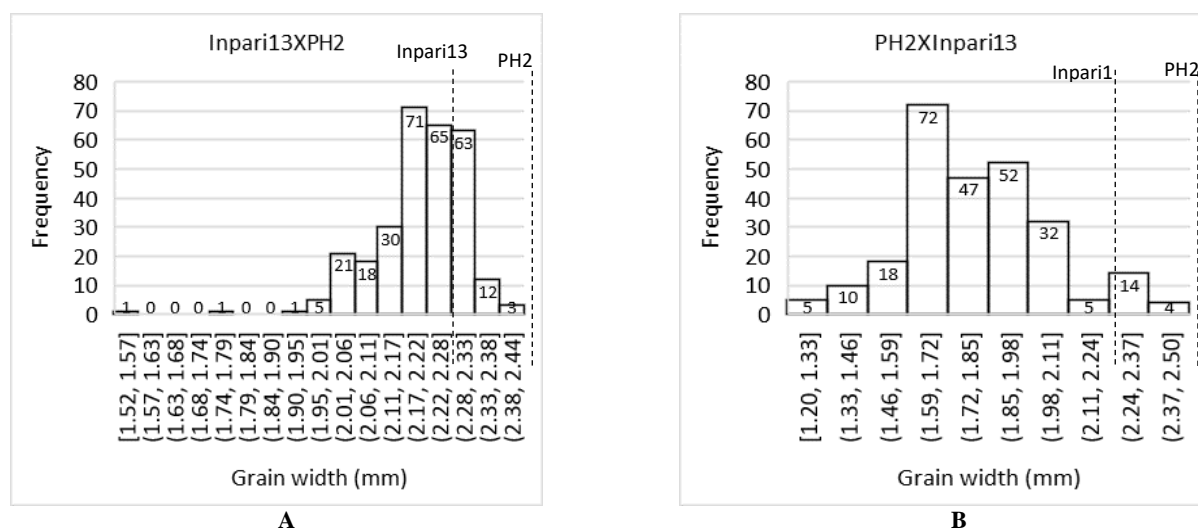

Figure 3. Variation of grain width from the F2 population of PH2 × Inpari 13 (A) and its reciprocal cross (B)
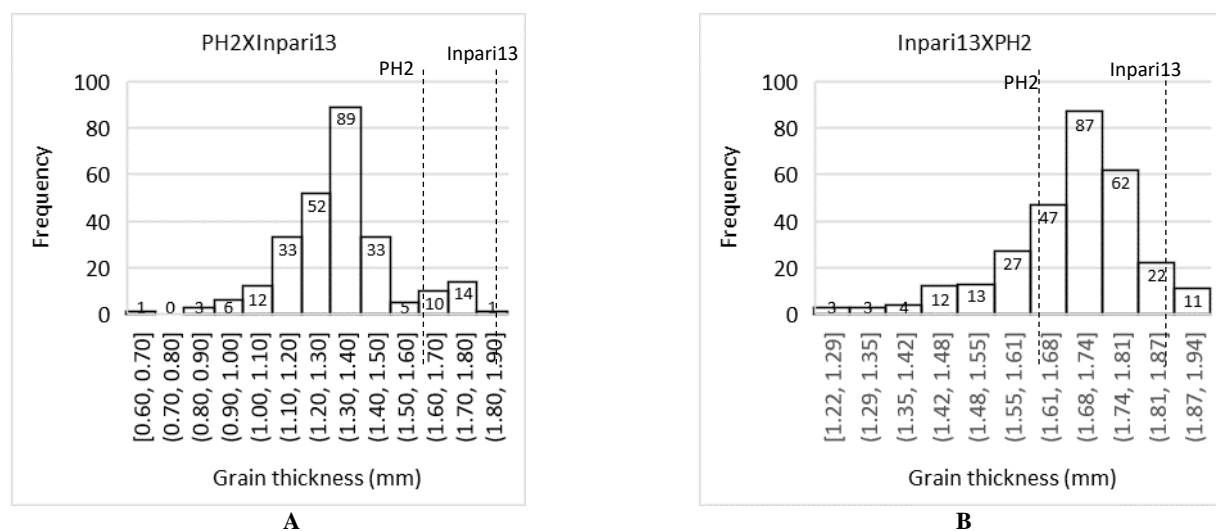

Figure 4. Variation of grain thickness from the F2 population of PH2 × Inpari 13 (A) and its reciprocal cross (B)

Table 4. Genetic variance of grain thickness of the parental genotypes, F2 generations of black × white rice genotypes, and their reciprocal crosses

Cross combination (pistil parent × pollen parent)	Pistil parent	Pollen parent	t-value parent	Mean of F2	t-value F2 – F2R	Range population of F2 generation (min-max)
PH2×Inpari 13	1.62±0.11	1.86±0.14	-20.26*	1.37±0.18	-24.44*	0.60–1.90
Inpari 13×PH2	1.86±0.14	1.62±0.11	20.26*	1.68±0.12		1.22–1.93
PH3× Inpari 13	1.57±0.13	1.86±0.14	-22.54*	1.67±0.16	0.65ns	1.10–1.90
Inpari 13×PH3	1.86±0.14	1.57±0.13	22.54*	1.66±0.13		1.23–2.29
PH4× Inpari 13	1.71±0.09	1.86±0.14	-14.2*	1.33±0.17	-27.47*	0.60–1.70
Inpari 13×PH4	1.86±0.14	1.71±0.09	14.2*	1.72±0.13		1.20–2.00
PH5× Inpari 13	1.63±0.12	1.86±0.14	-19.35*	1.14±0.26	-34.03*	0.50–1.60
Inpari 13×PH5	1.86±0.14	1.63±0.13	19.35*	1.70±0.16		1.06–2.02
PH8× Inpari 13	1.70±0.14	1.86±0.14	-12.94*	1.33±0.14	-37.41*	0.80–1.90
Inpari 13×PH8	1.86±0.14	1.70±0.14	12.94*	1.70±0.09		1.16–2.01
PH3× Inpari 18	1.57±0.13	1.84±0.11	-27.7*	1.31±0.18	-39.84*	0.40–2.20
Inpari 18×PH3	1.84±0.11	1.57±0.13	27.7*	1.83±0.10		1.26–2.13
PH4× Inpari 18	1.71±0.09	1.84±0.11	-15.14*	1.37±0.18	-36.49*	0.20–2.10
Inpari 18×PH4	1.84±0.11	1.71±0.09	15.14*	1.82±0.09		1.21–2.13
PH5× Inpari 18	1.63±0.12	1.84±0.11	-21.16*	1.38±0.19	-24.75*	0.50–2.30
Inpari 18×PH5	1.84±0.11	1.63±0.12	21.16*	1.72±0.11		1.17–1.99
PH8× Inpari 18	1.70±0.14	1.84±0.11	-13.04*	1.30±0.17	-38.00*	0.70–2.00
Inpari 18×PH8	1.84±0.11	1.70±0.14	13.04*	1.75±0.10		1.30–1.94
PH2× Inpari 19	1.62±0.11	1.80±0.08	-21.42*	1.69±0.10	-2.12*	1.20–1.90
Inpari 19×PH2	1.80±0.08	1.62±0.11	21.42*	1.71±0.09		1.27–2.30
PH3× Inpari 19	1.57±0.13	1.80±0.08	-26.04*	1.69±0.10	-1.78*	1.30–1.90
Inpari 19×PH3	1.80±0.08	1.57±0.13	26.04*	1.70±0.07		1.33–1.95
PH5× Inpari 19	1.63±0.12	1.80±0.08	-19.52*	1.70±0.12	-6.70*	1.10–2.00
Inpari 19×PH5	1.80±0.08	1.63±0.12	19.52*	1.75±0.07		1.37–1.98
PH6× Inpari 19	1.69±0.12	1.80±0.08	-12.2*	1.76±0.10	5.23*	1.30–2.00
Inpari 19×PH6	1.80±0.08	1.69±0.12	12.2*	1.72±0.08		1.40–1.90
PH7× Inpari 19	1.67±0.13	1.80±0.08	-13.97*	1.72±0.09	50.44*	1.40–1.90
Inpari 19×PH7	1.80±0.08	1.67±0.13	13.97*	1.27±0.13		1.00–1.70
PH8× Inpari 19	1.70±0.14	1.80±0.08	-9.54*	1.65±0.11	-5.57*	1.10–1.90
Inpari 19×PH8	1.80±0.08	1.70±0.14	9.54*	1.70±0.09		1.30–1.90

Note: F2: Filial 2, F2R: Reciprocal cross of F2, *: significant at level of 0.05; ns: not significant at level 0.05.

Gene action on the grain length, grain width, and grain thickness from the F2 populations of black × white rice genotypes and their reciprocal crosses

Most agronomic traits in rice are complex and polygenic (Yu et al. 2017). Each cross shows a different response. The research related to gene action in the important rice traits has been widely carried out. Carsono et al. (2014) reported that amylose level was inherited by simple genic and controlled by two pairs of genes with dominant and recessive (13: 1) epistasis gene action types in the cross of Ciherang × Pandanwangi and its reciprocal while Ciherang × Basmati was controlled by polygene. Estimation of gene action for grain length, grain width, and grain thickness from the F2 populations of black × white rice genotypes and their reciprocal crosses is shown in Tables 5, 6, and 7. Based on the skewness analysis, the grain length, grain width, and grain thickness are influenced by additive genes. Meanwhile, based on the results of the kurtosis test in all crosses, it can be seen that the genes that control the grain length, grain width, and grain thickness are influenced by polygene with additive types of gene action.

Inheritance pattern of grain color from the F2 populations of black × white rice genotypes and their reciprocal crosses

Indrasari (2016) stated that consumers choose type of rice for their consumption mainly due to nutritional and functional quality, with a percentage of 87% and 88% of respondents. Natural pigmented rice such as black rice is known to have more health benefits because of its anthocyanin content. The black rice trait is conferred by activation of the anthocyanin biosynthesis pathway in pericarps (Oikawa et al. 2015). The segregation pattern of an important character provides information on how selection can be made especially segregation pattern of the F2 generations (Rachmawati et al. 2020). Based on the results of the Chi-Square analysis on grain color, all crosses of black rice × white rice and its reciprocal crosses did not match the ratio of 1: 2: 1. This is different from the experiment conducted by Napitupulu and Damanhuri (2018), where an incomplete dominant gene controls the Javanese Melik × Pandan Wangi cross with a ratio of 1: 2: 1 and is not influenced by maternal effect. Based on Maeda et al. (2014) report, F2 population derived from a cross between the black rice NIL and 'Koshihikari' showed different results. The RM42441 genotype did not follow a 1: 2: 1 ratio, only the RM8129 and RM15191 genotypes had a 1: 2: 1 ratio.

Table 5. Gene action on grain length from the F2 populations of black × white rice genotypes and their reciprocal crosses

Cross	Skewness	SE.s	Zs	Type of gene action	Kurtosis	SE.k	Zk	Number of genes
PH2×Inpari 13	-1.32	-8.70	0.15	Additive	2.26	7.42	0.30	Polygene
PH3× Inpari 13	-0.76	-4.71	0.16	Additive	0.39	1.22	0.32	Polygene
PH4× Inpari 13	-0.60	-3.90	0.15	Additive	0.93	2.99	0.31	Polygene
PH5× Inpari 13	-0.54	-3.54	0.15	Additive	0.27	0.89	0.30	Polygene
PH8×Inpari 13	-0.27	-1.86	0.15	Additive	0.23	0.79	0.29	Polygene
Inpari 13×PH2	-0.44	-3.04	0.14	Additive	0.24	0.83	0.29	Polygene
Inpari 13×PH3	-0.16	-1.09	0.15	Additive	-0.43	-1.49	0.29	Polygene
Inpari 13×PH4	-2.08	-14.73	0.14	Additive	18.99	67.15	0.28	Polygene
Inpari 13×PH5	-0.64	-4.39	0.15	Additive	0.60	2.04	0.29	Polygene
Inpari 13×PH8	-0.30	-2.14	0.14	Additive	0.11	0.40	0.28	Polygene
PH3× Inpari 18	-0.34	-2.34	0.15	Additive	0.06	0.20	0.30	Polygene
PH4× Inpari 18	-0.55	-3.68	0.15	Additive	0.36	1.21	0.30	Polygene
PH5× Inpari 18	-0.44	-2.81	0.16	Additive	-0.75	-2.42	0.31	Polygene
PH8× Inpari 18	-0.71	-4.63	0.15	Additive	1.05	3.40	0.31	Polygene
Inpari 18×PH3	-2.31	-15.97	0.14	Additive	36.95	127.54	0.29	Polygene
Inpari 18×PH4	-0.53	-3.67	0.14	Additive	0.13	0.45	0.29	Polygene
Inpari 18×PH5	0.15	1.03	0.15	Additive	0.86	3.02	0.28	Polygene
Inpari 18×PH8	-0.35	-2.47	0.14	Additive	0.03	0.10	0.30	Polygene
PH2× Inpari 19	-0.39	-2.76	0.14	Additive	1.45	5.08	0.29	Polygene
PH3× Inpari 19	-1.11	-7.79	0.14	Additive	2.92	10.19	0.29	Polygene
PH5× Inpari 19	0.06	0.42	0.15	Additive	-0.28	0.97	0.29	Polygene
PH6× Inpari 19	-0.43	-2.95	0.15	Additive	0.60	2.06	0.29	Polygene
PH7× Inpari 19	-0.26	-1.76	0.15	Additive	0.50	1.68	0.30	Polygene
PH8× Inpari 19	0.31	2.12	0.15	Additive	2.88	9.74	0.30	Polygene
Inpari 19×PH2	-0.38	-2.63	0.14	Additive	-0.19	-0.65	0.29	Polygene
Inpari 19×PH3	-0.04	-0.29	0.14	Additive	-0.38	-1.34	0.28	Polygene
Inpari 19×PH5	-0.15	-1.02	0.15	Additive	-0.10	-0.36	0.28	Polygene
Inpari 19×PH6	-0.50	-3.54	0.14	Additive	0.82	2.88	0.28	Polygene
Inpari 19×PH7	-0.56	-3.82	0.15	Additive	0.50	1.70	0.29	Polygene
Inpari 19×PH8	-0.68	-4.77	0.14	Additive	0.58	2.02	0.29	Polygene

Note: Zs: skewness value; SEs: standard error of skewness; SEk: standard error of kurtosis; Zk: kurtosis value

Table 6. Gene action on grain width from the F2 populations of black × white rice genotypes and their reciprocal crosses.

Cross	Skewness	SE.s	Zs	Type of gene action	Kurtosis	SE.k	Zk	Number of genes
PH2×Inpari 13	0.28	1.85	0.15	Additive	0.36	1.18	0.31	Polygene
PH3× Inpari 13	-0.26	-1.58	0.16	Additive	1.88	5.63	0.33	Polygene
PH4× Inpari 13	-0.86	-5.54	0.16	Additive	2.21	7.14	0.31	Polygene
PH5× Inpari 13	-0.70	-4.57	0.15	Additive	-0.33	-1.08	0.31	Polygene
PH8×Inpari 13	-0.77	-5.32	0.14	Additive	0.86	2.97	0.29	Polygene
Inpari 13×PH2	-1.62	-11.28	0.14	Additive	7.03	24.49	0.29	Polygene
Inpari 13×PH3	-1.81	-12.62	0.14	Additive	22.19	77.12	0.29	Polygene
Inpari 13×PH4	-1.34	-9.45	0.14	Additive	6.53	23.07	0.28	Polygene
Inpari 13×PH5	-1.43	-9.74	0.15	Additive	3.47	11.80	0.29	Polygene
Inpari 13×PH8	0.39	2.77	0.14	Additive	8.55	30.20	0.28	Polygene
PH3× Inpari 18	-0.72	-5.02	0.14	Additive	0.24	0.82	0.29	Polygene
PH4× Inpari 18	-0.21	-1.38	0.15	Additive	1.27	4.26	0.30	Polygene
PH5× Inpari 18	-0.78	-5.04	0.15	Additive	1.76	5.69	0.31	Polygene
PH8× Inpari 18	-1.14	-7.38	0.15	Additive	1.55	5.01	0.31	Polygene
Inpari 18×PH3	-0.83	-5.72	0.15	Additive	1.88	6.46	0.29	Polygene
Inpari 18×PH4	-0.65	-4.49	0.14	Additive	3.77	13.02	0.29	Polygene
Inpari 18×PH5	-0.90	-6.34	0.14	Additive	0.87	3.06	0.28	Polygene
Inpari 18×PH8	-0.36	-2.51	0.14	Additive	4.43	15.64	0.28	Polygene
PH2× Inpari 19	-0.58	-4.09	0.14	Additive	0.14	0.48	0.29	Polygene
PH3× Inpari 19	-0.17	-1.20	0.14	Additive	-0.27	-0.93	0.29	Polygene
PH5× Inpari 19	-0.01	-0.07	0.14	Additive	-0.10	-0.33	0.30	Polygene
PH6× Inpari 19	-0.58	-3.98	0.15	Additive	0.41	1.40	0.29	Polygene
PH7× Inpari 19	-0.69	-4.66	0.15	Additive	1.73	5.87	0.29	Polygene
PH8× Inpari 19	-0.76	-5.13	0.15	Additive	1.24	4.18	0.30	Polygene
Inpari 19×PH2	-1.24	-8.50	0.15	Additive	2.66	9.14	0.29	Polygene
Inpari 19×PH3	0.05	0.37	0.14	Additive	4.50	15.76	0.29	Polygene
Inpari 19×PH5	0.19	1.27	0.15	Additive	-0.27	-0.93	0.29	Polygene
Inpari 19×PH6	-0.93	-6.58	0.14	Additive	2.37	8.37	0.28	Polygene
Inpari 19×PH7	-0.21	-1.41	0.15	Additive	-0.33	-1.14	0.29	Polygene
Inpari 19×PH8	-0.62	-4.38	0.14	Additive	0.31	1.07	0.29	Polygene

Note: Zs: skewness value; SEs: standard error of skewness; SEk: standard error of kurtosis; Zk: kurtosis value

Table 7. Gene action on grain thickness from the F2 populations of black × white rice genotypes and their reciprocal crosses.

Cross	Skewness	SE.s	Zs	Type of gene action	Kurtosis	SE.k	Zk	Number of genes
PH2×Inpari 13	-0.02	-0.10	0.20	Additive	1.50	4.92	0.30	Polygene
PH3× Inpari 13	-1.54	-9.51	0.16	Additive	2.12	6.55	0.32	Polygene
PH4× Inpari 13	-1.24	-7.98	0.16	Additive	2.73	8.82	0.31	Polygene
PH5× Inpari 13	-0.64	-4.19	0.15	Additive	-0.84	-2.73	0.31	Polygene
PH8×Inpari 13	0.70	4.81	0.15	Additive	3.65	12.57	0.29	Polygene
Inpari 13×PH2	-0.95	-6.59	0.14	Additive	1.51	5.24	0.29	Polygene
Inpari 13×PH3	-0.64	-4.48	0.14	Additive	2.77	9.64	0.29	Polygene
Inpari 13×PH4	-0.51	-3.64	0.14	Additive	0.63	2.23	0.28	Polygene
Inpari 13×PH5	-1.61	-10.99	0.15	Additive	2.88	9.79	0.29	Polygene
Inpari 13×PH8	-1.52	-10.74	0.14	Additive	8.71	30.73	0.28	Polygene
PH3× Inpari 18	1.07	7.44	0.14	Additive	6.96	24.14	0.29	Polygene
PH4× Inpari 18	-0.23	-1.58	0.15	Additive	7.79	26.23	0.30	Polygene
PH5× Inpari 18	-0.05	-0.33	0.15	Additive	3.45	11.12	0.31	Polygene
PH8× Inpari 18	0.57	3.69	0.15	Additive	2.69	8.73	0.31	Polygene
Inpari 18×PH3	-2.57	-17.75	0.14	Additive	11.63	40.16	0.29	Polygene
Inpari 18×PH4	-1.91	-13.18	0.14	Additive	10.62	36.71	0.29	Polygene
Inpari 18×PH5	-1.02	-7.15	0.14	Additive	2.74	9.62	0.28	Polygene
Inpari 18×PH8	-1.43	-10.09	0.14	Additive	3.42	12.07	0.28	Polygene
PH2× Inpari 19	-1.03	-7.22	0.14	Additive	3.14	11.02	0.28	Polygene
PH3× Inpari 19	-0.38	-2.69	0.14	Additive	0.73	2.55	0.29	Polygene
PH5× Inpari 19	-0.90	-6.18	0.15	Additive	2.47	8.54	0.29	Polygene
PH6× Inpari 19	-1.12	-7.65	0.15	Additive	2.48	8.48	0.29	Polygene
PH7× Inpari 19	-0.73	-4.93	0.15	Additive	0.89	3.01	0.30	Polygene
PH8× Inpari 19	-1.06	-7.19	0.15	Additive	3.43	11.61	0.30	Polygene
Inpari 19×PH2	-0.24	-1.67	0.14	Additive	9.15	31.41	0.29	Polygene
Inpari 19×PH3	-0.30	-2.13	0.14	Additive	2.40	8.41	0.29	Polygene
Inpari 19×PH5	-0.29	-1.95	0.15	Additive	2.49	8.46	0.29	Polygene
Inpari 19×PH6	-0.73	-5.15	0.14	Additive	1.84	6.50	0.28	Polygene
Inpari 19×PH7	0.41	2.78	0.15	Additive	0.16	0.53	0.30	Polygene
Inpari 19×PH8	-1.07	-7.54	0.14	Additive	2.93	10.28	0.29	Polygene

Note: Zs: skewness value; SEs: standard error of skewness; SEk: standard error of kurtosis; Zk: kurtosis value

Estimation of the components of genetic variance and heritability

The heritability of the broad meaning and the narrow meaning is used to facilitate plant breeding programs because there is a correlation between genetics and phenotypes (Haryanto et al. 2017). According to Dewi et al. (2019), diverse genetic material can increase the chances of getting the desired gene in the plants to be incorporated. Genetic variance is required in calculating heritability. According to Singh et al. (2020), heritability refers to the ratio of genotypic variance to phenotypic. The results showed that the variance at each cross gave different responses. According to Table 8, it can be seen that the broad-sense heritability of black rice genotypes crossed with Inpari 13 and its reciprocal crosses ranged from 0 to 75.19%, while black rice genotypes crossed with Inpari 18 and its reciprocal ranged from 0 to 71.53%, and black rice genotypes crossed with Inpari 19 ranged from 0 to 36.57%. The crosses of PH2 × Inpari 13, PH4 × Inpari 13, and PH5 × Inpari 13 have a high broad meaning heritability value of more than 50% for grain length, grain width, and grain thickness. Gupta et al. (2020) stated that high heritability is probably due to the influence of additive genes. The genetic variance in each combination also has a different value where the cross of PH5 × Inpari 13 has the highest genetic variance at 19.67%.

Table 8. Chi-square analysis on grain color from the F2 populations of black × white rice genotypes and their reciprocal crosses

Cross	Observed phenotype			Expected phenotype			Σ	(O-E)²/E	(O-E)²/E	(O-E)²/E	χ²
	P	B	W	P	B	W					
PH2×Inpari 13	194	4	0	50	99	50	198	105	46	12	163
PH3× Inpari 13	205	26	14	61	123	61	245	84	38	9	131
PH4× Inpari 13	200	23	0	56	112	56	223	93	35	14	142
PH5× Inpari 13	240	0	0	60	120	60	240	135	60	15	210
PH8×Inpari 13	203	52	0	64	128	64	255	76	22	16	114
Inpari 13×PH2	247	0	0	62	124	62	247	139	62	15	216
Inpari 13×PH3	242	12	0	64	127	64	254	125	52	16	193
Inpari 13×PH4	270	0	0	68	135	68	270	152	68	17	236
Inpari 13×PH5	0	163	30	48	97	48	193	12	23	2	37
Inpari 13×PH8	65	227	0	73	146	73	292	0	22	18	41
PH3× Inpari 18	119	171	0	73	145	73	290	7	2	18	28
PH4× Inpari 18	280	23	0	76	152	76	303	138	54	19	211
PH5× Inpari 18	13	264	0	69	139	69	277	11	57	17	86
PH8× Inpari 18	201	87	0	72	144	72	288	58	11	18	87
Inpari 18×PH3	0	0	300	75	150	75	300	19	75	169	263
Inpari 18×PH4	194	4	0	50	99	50	198	105	46	12	163
Inpari 18×PH5	205	26	14	61	123	61	245	84	38	9	131
Inpari 18×PH8	200	23	0	56	112	56	223	93	35	14	142
PH2× Inpari 19	240	0	0	60	120	60	240	135	60	15	210
PH3× Inpari 19	203	52	0	64	128	64	255	76	22	16	114
PH5× Inpari 19	247	0	0	62	124	62	247	139	62	15	216
PH6× Inpari 19	242	12	0	64	127	64	254	125	52	16	193
PH7× Inpari 19	270	0	0	68	135	68	270	152	68	17	236
PH8× Inpari 19	0	163	30	48	97	48	193	12	23	2	37
Inpari 19×PH2	65	227	0	73	146	73	292	0	22	18	41
Inpari 19×PH3	119	171	0	73	145	73	290	7	2	18	28
Inpari 19×PH5	280	23	0	76	152	76	303	138	54	19	211
Inpari 19×PH6	13	264	0	69	139	69	277	11	57	17	86
Inpari 19×PH7	201	87	0	72	144	72	288	58	11	18	87
Inpari 19×PH8	0	0	300	75	150	75	300	19	75	169	263

Note: P: purple, B: brown, W: white, O: observed, E: expected number, χ² table: 5.99

Table 9. Component of variance and heritability of grain length, grain width, and grain thickness of F2 populations of black × white rice genotypes and their reciprocal crosses

Cross	Grain length					Grain width					Grain thickness				
	σ^2_P	σ^2_E	σ^2_G	h^2	CVG	σ^2_P	σ^2_E	σ^2_G	h^2	CVG	σ^2_P	σ^2_E	σ^2_G	h^2	CVG
PH2×Inpari 13	0.06	0.01	0.04	77.01	11.68	0.03	0.02	0.02	52.96	9.71	0.03	0.02	0.02	52.96	9.71
PH3× Inpari 13	0.58	0.02	0.56	96.69	30.66	0.02	0.02	0.00	11.69	2.22	0.03	0.02	0.01	31.81	5.48
PH4× Inpari 13	0.04	0.02	0.02	52.59	7.52	0.03	0.01	0.02	55.84	9.35	0.03	0.01	0.02	55.84	9.35
PH5× Inpari 13	0.07	0.02	0.05	75.06	13.73	0.07	0.02	0.05	75.19	19.76	0.07	0.02	0.05	75.19	19.76
PH8×Inpari 13	0.02	0.02	0.01	33.47	4.89	0.02	0.02	0.00	0.61	0.83	0.02	0.02	0.00	0.61	0.83
Inpari 13×PH2	0.01	0.01	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00
Inpari 13×PH3	0.01	0.02	-0.01	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00
Inpari 13×PH4	0.01	0.02	-0.01	0.00	0.00	0.02	0.01	0.01	32.80	4.49	0.02	0.01	0.01	32.80	4.49
Inpari 13×PH5	0.02	0.02	0.01	28.29	3.57	0.02	0.02	0.01	30.79	5.08	0.02	0.02	0.01	30.79	5.08
Inpari 13×PH8	0.01	0.02	-0.01	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.02	-0.01	0.00	0.00
PH3× Inpari 18	0.15	0.17	-0.02	0.00	0.00	0.05	0.02	0.03	55.35	8.79	0.03	0.01	0.02	58.38	10.63
PH4× Inpari 18	0.20	0.23	-0.03	0.00	0.00	0.04	0.02	0.03	56.93	8.34	0.03	0.01	0.02	71.53	11.23
PH5× Inpari 18	0.50	0.25	0.25	49.69	7.38	0.05	0.02	0.04	65.26	9.87	0.04	0.01	0.02	65.41	11.32
PH8× Inpari 18	0.19	0.21	-0.01	0.00	0.00	0.06	0.02	0.04	67.06	10.49	0.03	0.02	0.01	44.95	8.54
Inpari 18×PH3	0.21	0.17	0.04	16.99	2.81	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Inpari 18×PH4	0.14	0.23	-0.09	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Inpari 18×PH5	0.16	0.25	-0.09	0.00	0.00	0.02	0.02	0.00	11.27	2.15	0.01	0.01	0.00	0.00	0.00
Inpari 18×PH8	0.12	0.21	-0.08	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.02	-0.01	0.00	0.00
PH2× Inpari 19	0.10	0.12	-0.02	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.00	4.30	1.22
PH3× Inpari 19	0.14	0.12	0.02	15.00	2.25	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00
PH5× Inpari 19	0.16	0.17	-0.01	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	0.00	26.82	3.58
PH6× Inpari 19	0.13	0.15	-0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.00	7.87	1.63
PH7× Inpari 19	0.12	0.17	-0.05	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00
PH8× Inpari 19	0.12	0.14	-0.02	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	0.00	1.61	0.84
Inpari 19×PH2	0.08	0.12	-0.04	0.00	0.00	0.02	0.01	0.01	37.98	4.02	0.01	0.01	0.00	0.00	0.00
Inpari 19×PH3	0.10	0.12	-0.02	0.00	0.00	0.01	0.02	-0.01	0.00	0.00	0.01	0.01	-0.01	0.00	0.00
Inpari 19×PH5	0.14	0.17	-0.03	0.00	0.00	0.02	0.02	0.00	10.16	1.92	0.01	0.01	0.00	0.00	0.00
Inpari 19×PH6	0.09	0.15	-0.06	0.00	0.00	0.01	0.01	-0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Inpari 19×PH7	0.15	0.17	-0.02	0.00	0.00	0.04	0.02	0.03	60.16	9.27	0.02	0.01	0.01	36.57	6.15
Inpari 19×PH8	0.16	0.14	0.02	9.74	1.85	0.01	0.02	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00

Note: σ^2_P: phenotypic variance, σ^2_G: genotypic variance, σ^2_E: environmental variance, h^2_{bs}: broad-sense heritability; CGV: coefficient of genotypic variance

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