RESEARCH ARTICLE

SABRAO Journal
of Breeding and Genetics
50 (1) 9-24, 2018

ANALYSIS OF PANICLE MORPHOLOGY TRAITS IN F2 AND RECIPROCAL F2 POPULATIONS OF RICE (*Oryza sativa* L.)

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SUMMARY

Panicle morphology varies widely among rice genotypes, however genetic analysis reports for this trait are lacking. This study aimed to observe and investigate the variability and heritability of panicle morphology characters in F2 and F2 reciprocal (F2-R) populations. Two rice genotypes which differed in eights panicle characters were crossed. The F1 and F2 populations were generated and planted in the dry season 2016 (F1 populations) and the rainy season 2017 (F2 populations). The results indicated that the estimated broad-sense heritability was high for number of primary branches, secondary branches, and tertiary branches, spikelets, panicles and panicle axis length and ranged from 0.57 to 0.97 in both F2 and F2-R populations. Gene action was observed to be additive in the both populations, with additional complementary epistasis for numbers of panicles, secondary branches, and spikelets but not for grain initiation length and primary branches. All characters observed were controlled by minor genes in both F2 and F2-R populations except for number of panicles in the F2-R population. The genetic advance was high for primary branches, secondary branches, tertiary branches, spikelet number and panicle number in both F2 and F2-R populations, as well as for grain initiation length and panicle axis length in the F2 population. Correlation analysis revealed highly significant positive correlations between all panicle characters observed except grain initiation length and panicle number in both F2 and F2-R populations. This study provided information on the heritability and relationships between panicle characters to develop new high-yielding rice cultivars.

Key words: Additive gene, heritability, panicle branches

Key findings: The study revealed that was no matternal effect on panicle characters performance investigated in F1 populations. Tertiary branching as well

secondary and primary branching were important to increase panicle size related to heavy panicles.

Manuscript received: December 15, 2017; Decision on manuscript: December 23, 2017; Accepted: February 7, 2018.

Communicating Editor: Dr. Sobir

INTRODUCTION

Rice productivity is determined by agronomic and morphological trait performance. Therefore the improvement of plant morphology traits has played an important role in increasing the yield potential of rice. Rice breeding for super high yield depends on large panicles, panicles with many branches and spikelets and both large panicles per unit area and spikelet number (Min *et al*., 2011; Zheng *et al*., 2006). Rice yield is divided into sink size (panicle architecture or grain size) and source potential whether mostly determined by tiller number and panicle morphology, which are generally regarded as key factors (He *et al*., 2010; Wang and Li, 2011). The morphological components and developmental characteristics of a rice panicle are genetically determined (Yamagishi *et al*., 2004). Rice tillers are specialized branches bearing panicles, which are composed of primary branches, secondary branches, tertiary branches and grains. Four panicle types were characterized: compact, intermediate, loose, and chicken foot panicle for which considerable differences existed, especially in panicle length, the secondary branch number and panicle density (Cheng *et al*., 2014).

Processes of rice panicle morphogenesis consist of primary branch formation, floret differentiation on each branch, and floret development (Yamagishi *et al*., 2004). In addition, three factors were suggested to be involved with grain-filling; (1) dry matter production during the ripening period, (2) the unfertilized spikelet due to the large number of spikelet per panicle and (3) the mobilization of the non-structural carbohydrate (Yoshinaga *et al*., 2013). Rice panicle morphogenesis begins around 1 month before anthesis with branch development (Bommert *et al*., 2005). The primary branch differentiate in a spiral phyllotaxy on the inflorescence meristem then produces 10–50 florets subsequently, as well as several axillary secondary branches and tertiary branches in some genotypes (Kato and Katsura 2010, Sheehy et *al*., 2001). Earlier reports revealed that the level of rice yield has a significant difference in the mean value of primary branches: 11-14 for the high-yielding varieties, 8-12 for the low-yielding type, while mostly 10-13 for the medium- yielding variety (Zheng *et al*., 2006).

The morphological and physiological traits, which improved filling efficiency in large-panicle rice varieties, are critical to devise strategies for breeding programs (Yao *et al*., 2016). Therefore, the desired plant characters could be mostly achieved by hybridization of two distinct parentss and studied by observing segregation in the F2 population. The crosses between the genotypes with maximum genetic divergence would be important for

improvement due to yield desirable recombinants in the progeny. Moreover, genetic variability studies provide an information of genetic parameters based on which selection of genotypes and breeding strategy could be useful for crop improvement (Kahani and Hittalmani, 2015). High heritability and genetic advances will further improve the efficacy of selection to determine progress or response to selection of the characters (Lestari *et al*., 2015). In addition, by performing correlation analysis will provide reliable information on the consequences of selection for simultaneous improvement of desirable yield component characters (Venkanna *et al*., 2014). Nevertheless the genetic identification of rice traits has been challenging because heredity of traits controlled by polygenes is complex (Hao and Lin, 2010).

Recently, the physiological mechanisms and genetic basis of the erect and large panicle super-high-yield rice type model were analysed mainly on the panicle type, number of large vascular bundles in the panicle neck, and the panicle type index (Jin *et al*., 2010). Another study on panicle morphology was done to develop the models for predicting the dynamics of panicle geometric morphology, panicle and branch curves and panicle colour, and to visualize rice panicle in three dimensions (Zhang *et al*., 2014) and develop software called P-Trap (Panicle Trait Phenotyping tool) (Faroq *et al*., 2013). In addition, branching in rice was investigated past year by finding the gene *MONOCULM 1* (*MOC* 1) characterized as a key regulator in controlling rice tillering and branching, which offers potential to identify important genes associated with grain yield, elucidating the genetic basis of yield-related trait (Liang *et al*., 2014). Nevertheless further field experiments are necessary for validation.

At present, research on panicle morphology characters to develop new high-yielding varieties has been rarely found. Therefore in this study, the panicle characteristics of the F2 segregating populations and their relationships were investigated. The objectives of this study were to observe the variability and heredity of rice panicle morphology characters in F2 population.

MATERIALS AND METHODS

Genetic materials and experimental design

The crossing of two parents and its reciprocal were conducted at the Micro Technic Laboratory of Bogor Agricultural University, focused on their distinct panicle characters (Figure 1). Two parents had panicle morphological differences based on visual inspection particularly on panicle length and number of branches (primary, secondary and tertiary). The genotypes used in this study were IPB175-F-7-1-1 (P1) and IPB175-F-31-2-1 (P2) (Figure 2). The crossing between IPB175-F-7-1-1 (female) and IPB175-F-31-2-1 (male) generated the F1 and, F2 populations as well. Subsequently, a reciprocal crossing was performed to generate the F1R and F2-R populations. A randomized complete block design with two replications were applied. The F1 generations were planted at Sawah Baru Babakan, Bogor from February to June 2016 (dry season). Then the F2 segregating populations were evaluated from October 2016 to February 2017 (rainy season) in plots of 2 m x 10 m with space 25 cm

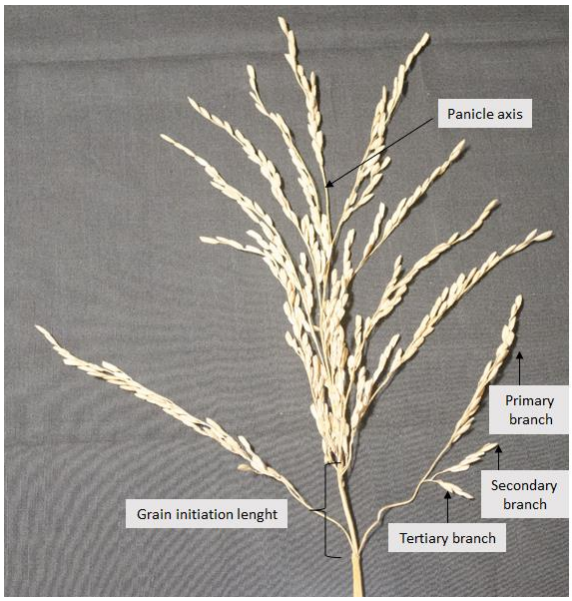

Figure 1. Panicle morphology of rice consist of Primary Branch (PB), Secondary Branch (SB), Tertiary Branch (TB), Grain Initiation length (GI), and Panicle Axis length (PA).

Figure 2. Phenotype of panicle morphology both parents used as plant crossing materials. Bar = 2 cm.

between the plants where one seed from each hill. The plants were fertilized with 207, 36 and 45 kg ha^{-1} of N, P and K, respectively.

Statistical analysis

All the biometrical of panicle observations were recorded on 150 randomly selected plant samples for each population on panicle length (PL, cm), primary branches (PB), secondary branches (SB), tertiary branches (TB), panicle axis length (PA, cm), grain initiation length (GI, cm), spikelet number per panicle (SN), and panicle number per plant (PN). The panicle morphology was evaluated in

three random panicles from each plant with totally 150 plants from each F2 and F2-R populations. This referred to our previous study of sampling method of panicle morphology experiment (data not shown). The estimates of heritability, genetic coefficients of variability, genetic advance, gene action, number of genes and correlation analysis was computed in F2 and F2-R segregating populations. Statistical analyses were performed using Minitab 17 and Star. For mean separation and comparison between populations, t- test was used.

Broad-sense heritability

Broad-sense heritability was estimated for F2 and F2-R respectively (Singh and Chaudhary, 1979).

$$h^2_{bs} = \frac{\sigma^2_g}{\sigma^2_p}$$

$$\sigma^2_p = \sigma^2_{F2}$$

$$\sigma^2_e = \frac{\sigma^2_{P1} + \sigma^2_{P2}}{2}$$

$$\sigma^2_g = \sigma^2_p - \sigma^2_e$$

h^2_{bs} = broad-sense heritability, σ^2= variance, σ^2_g = genetic variance, *xi* = observed value, σ^2_e = environment variance, n = number of observation, σ^2_p = parent variance.

There were three heritability classes, i.e.: high (h^2 > 0.5), moderate (0.2 < h^2 < 0.5), low (h^2 < 0.2) (Stansfield, 1991).

Genetic coefficient of variation

$$GCV = \frac{\sqrt{\sigma^2_g}}{\bar{X}} x100\%$$

There were three criteria (Knight, 1979): narrow (0-10%), moderate (10-20%) and broad (>20%).

Genetic advance

$$GA = i \times h^2 \times \sigma_p$$

i=selection intensity, 10%=1.76

$$GAM = \frac{GA}{\bar{X}} x\ 100\ \%$$

0<GA<3.3% = low, 3.3% <GA<6.6% = medium-low, 6.6% <GA<10% = medium-high, GA>10% = high (Widyawati *et al*., 2014).

Number and gene action

Skewness and kurtosis

$$Skewness = \frac{\sum_{i=1}^{N}(Yi-Y)^3}{(N-1)s^3}$$

Skewness value shows epistasis that effected expression of a character. If Zs was significant, it shows epistasis while it in contrast, there is additive gene action. Skewness > 0 indicates a complimentary epistasis gene action, whether skewness < 0, there is a duplicate epistasis gene action (Lestari *et al.,* 2015).

$$Kurtosis = \frac{\sum_{i=1}^{N}(Yi-Y)^4}{(N-1)s^4}$$

Kurtosis shows number of gene that controlling a character. If Kurtosis>3, it means character is controlled by a few gene while Kurtosis < 3, the character is controlled by many genes (Roy, 2000).

Correlation analysis

The correlation between traits were observed using Pearson correlation

method. Correlation analysis (Gaspersz, 1992):

$$r_{xy} = \frac{n\sum x_i y_i - (\sum x_i)(\sum y_i)}{\sqrt{[n\sum x_i^2 - (\sum x_i)^2][(n\sum y_i^2 - (\sum y_i)^2]}}$$

r_{xy} = correlation variable, X and Y; n= number of observation; x = variable value X; and y = variable value Y.

RESULTS

Phenotypic performance of parents and F1 generations

The variability of panicle characters was an interesting parameter that needs to be investigated. Both F1 and F1R populations had no significant difference for all panicle characters observed (Table 1). Nevertheless, F1R population had a higher phenotypic mean value for all characters than F1 except primary branches. P1 and P2 had a highly significant difference for most of panicle characters observed except for grain inititation lenght (Table 2). P2 had generally higher value for all panicle traits than P1 except panicle numbers.

Panicle morphology traits of F2 and F2-R populations

Primary branches

Primary branches mean value in F2 and F2-R population were 11.89 and 15.28, that were between their parents (14.15 and 14.39) respectively (Table 2). It was a high broad-sense heritability (0.91) associated with high genetic advance (14.64) were estimated in F2 and F2-R populations (Table 3). This panicle characters had an additive gene action with multiple gene controlled that were similar in both populations (Tables 4 and 5). Futhermore, the correlation analysis revealed that primary branches was a highly significant positive correlation within all characters observed except panicle number (Table 6).

Secondary branches

The F2 and F2-R progenies distribution showed that secondary branches were 41.46 and 35.8 which were more higher than their parents (26.28 and 34.17) respectively (Table 2). Moreover, it revealed high broad-sense heritability (0.95 and 0.87) as well as genetic advance (43.34 and 26.90), whereas a genetic coefficient variation showed a broad criteria (25.22) and moderate (16.42) in F2 nd F2-R populations respectively (Table 3). Based on the skewness and kurtosis values, this character was controlled by many genes as additive with complementary epistasis gene action in both F2 and F2-R populations (Tables 4 and 5). Most of traits observed had a highly significant positive correlation with secondary branches. In contrast for panicle number and grain initiation length in both populations, there was no significant correlation with secondary branches (Table 6).

Tertiary branches

Unexpected F2 and F2-R progenies distribution for tertiary branches were observed. The F2 and F2-R populations achieved 6.41 and 5.63 on average for these characters compared with their parents (1.67 and 3.83) respectively. Even though high variation occurred in each population.

Table 1. Mean values of panicle characters of F1 generation planted at Sawah Baru Babakan, Bogor in dry season 2016.

Variables	F1	F1R	P-value
PB	15.11 ± 2.27	13.78 ± 0.39	0.37
SB	41.44 ± 10.71	42.00 ± 4.33	0.93
TB	6.89 ± 4.19	7.78 ± 1.17	0.74
SN	297.67 ± 78.26	323.11 ± 32.01	0.62
PN	29.00 ± 7.00	30.33 ± 0.58	0.77
PL (cm)	28.11 ± 1.65	28.89 ± 1.07	0.53
GI (cm)	1.11 ± 0.48	1.61 ± 0.42	0.24
PA (cm)	22.11 ± 1.95	24.22 ± 1.07	0.17

PB=Primary Branch, SB=Secondary Branch, TB = Tertiary Branch, SN=Spikelet Number, PN=Panicle Number, PL=Panicle Length, GI=Grain Initiation length, PA=Panicle Axis length. T-test ($P < 0.05$).

Table 2. Mean values of panicle characters of parents and progenies distribution of F2 and F2-R populations planted at Sawah Baru Babakan Bogor in rainy season 2016-2017.

Variable	P			F2		
	P1	P2	P-value	F2	F2-R	P-value
PB	11.89 ± 0.34	15.28 ± 0.44	0.00	14.15 ± 1.30	14.39 ± 1.17	0.19
SB	26.28 ± 1.71	34.17 ± 2.78	0.00	41.46 ± 10.71	35.80 ± 6.31	0.00
TB	1.67 ± 0.37	3.83 ± 1.03	0.00	6.41 ± 4.56	5.63 ± 2.10	0.08
SN	186.22 ±18.10	253.16 ± 31.07	0.00	275.90 ± 60.50	271.30 ± 51.32	0.19
PN	11.17 ± 1.17	9.17 ± 0.75	0.01	8.27 ± 2.69	9.03 ± 3.11	0.03
PL (cm)	24.50 ± 0.81	29.00 ± 1.99	0.00	26.91 ± 2.27	27.20 ± 1.85	0.39
GI (cm)	2.17 ± 0.62	2.39 ± 0.77	0.60	2.23 ± 0.65	2.33 ± 0.63	0.35
PA (cm)	17.11 ± 0.64	19.22 ± 0.94	0.00	22.00 ± 2.11	21.88 ± 1.70	0.38

PB=Primary Branch, SB=Secondary Branch, TB = Tertiary Branch, SN=Spikelet Number, PN=Panicle Number, PL=Panicle Length, GI=Grain Initiation length, PA=Panicle Axis length. T-test ($P<0.05$).

Table 3. Estimates of heritability (broad-sense), GCV and GA% mean in F2 and F2-R populations, rainy season 2016-2017.

Variable	F2 Population				F2-R Population			
	σg	h^2bs	GCV	%GA	σg	h^2bs	GCV	%GA
PB	1.53	0.91	8.74	14.64	1.21	0.88	7.64	12.64
SB	109.29	0.95	25.22	43.34	34.55	0.87	16.42	26.90
TB	20.18	0.97	70.07	21.55	3.81	0.86	34.65	56.71
SN	3014.14	0.82	19.90	31.78	1987.31	0.75	16.43	25.12
PN	6.27	0.87	30.28	49.59	8.67	0.90	32.61	54.43
PL (cm)	2.85	0.55	6.27	8.20	1.12	0.33	3.88	3.90
GI (cm)	0.09	0.20	13.07	10.23	0.06	0.14	10.07	6.57
PA (cm)	3.24	0.73	8.18	12.27	1.68	0.58	5.92	7.94

PB=Primary Branch, SB=Secondary Branch, TB = Tertiary Branch, SN=Spikelet Number, PN=Panicle Number, PL=Panicle Length, GI=Grain Initiation length, PA=Panicle Axis length.

Table 4. Estimation of number and genes actions in F2 segregating population, rainy season 2016-2017.

Variables	Skewness	Kurtosis	Zs	Zk	Gene action	Gene number
PB	0.06	0.00	0.32 ^{ns}	0.00 ^{ns}	Additive	Many
SB	0.83	0.41	4.39**	1.08 *	Additive, complementary epistasis	Many
TB	1.29	2.09	6.83**	5.53**	Additive, complementary epistasis	Many
SN	0.60	0.79	3.17**	2.09**	Additive, complementary epistasis	Many
PN	0.88	1.99	4.66**	5.26**	Additive, complementary epistasis	Many
PL	-0.42	1.43	-2.22**	3.78**	Additive, duplicate epistasis	Many
GI	-0.03	-0.54	-0.16^{ns}	-1.42 ^{ns}	Additive	Many
PA	0.42	1.06	2.22**	2.80**	Additive, complementary epistasis	Many

PB=Primary Branch, SB=Secondary Branch, TB = Tertiary Branch, SN=Spikelet Number, PN=Panicle Number, PL=Panicle Length, GI=Grain Initiation length, PA=Panicle Axis length. Kurtosis > 3 = a few gene, Kurtosis < 3 = many genes. * and ** = significant at $P < 0.01$ and at $P < 0.05$; ns = not significant.

Table 5. Estimation of number and genes actions in F2-R segregating population, rainy seasons 2016-2017.

Variables	Skewness	Kurtosis	Zs	Zk	Gene action	Gene number
PB	0.32	-0.45	1.58 ^{ns}	-1.11 ^{ns}	Additive	Many
SB	0.79	1.01	3.91**	2.49**	Additive, complementary epistasis	Many
TB	0.43	-0.07	2.12 ^{ns}	-0.17 ^{ns}	Additive	Many
SN	0.82	0.81	3.95**	1.97**	Additive, complementary epistasis	Many
PN	1.49	3.93	7.37**	9.72**	Additive, complementary epistasis	Few
PL	-0.23	0.95	-1.13 ^{ns}	2.35**	Additive, duplicate epistasis	Many
GI	-0.39	-0.64	-1.93 ^{ns}	-1.58 ^{ns}	Additive	Many
PA	-0.74	2.95	-3.66**	7.30**	Additive, duplicate epistasis	Many

PB=Primary Branch, SB=Secondary Branch, TB = Tertiary Branch, SN=Spikelet Number, PN=Panicle Number, PL=Panicle Length, GI=Grain Initiation length, PA=Panicle Axis length. Kurtosis > 3 = a few gene, Kurtosis < 3 = many genes. ** = significant at $P < 0.01$; ns = not significant.

Table 6. Pearson correlation among panicle morphological characters of F2 population (below diagonal) and F2-R population (above diagonal), rainy season 2016-2017.

	PB	SB	TB	SN	PN	PL	GI	PA
PB		0.38**	0.28**	0.43**	-0.03	0.32**	0.17*	0.52**
SB	0.51**		0.75**	0.88**	0.02	0.32**	-0.15	0.38**
TB	0.35**	0.68**		0.75**	0.11	0.20*	-0.16*	0.31**
TB	0.60**	0.77**	0.54**		0.05	0.34**	-0.17*	0.47**
PN	0.09	0.07	-0.02	0.06		0.16	-0.05	0.16*
PL	0.48**	0.30**	0.22**	0.42**	0.22**		0.03	0.44**
GI	0.24**	0.07	-0.01	0.02	0.10	0.07		0.03
PA	0.53**	0.39**	0.29**	0.49**	0.09	0.87**	0.04	

PB=Primary Branch, SB=Secondary Branch, TB = Tertiary Branch, SN=Spikelet Number, PN=Panicle Number, PL=Panicle Length, GI=Grain Initiation length, PA=Panicle Axis length. *significant correlation ($P < 0.05$), **highly significant correlation ($P < 0.01$).

High broad-sense heritability (0.97 and 0.86) was observed as well as a broad genetic coefisient variation (21.55 and 56.71) in F2 and F2-R populations respectively. Surprisingly, a high genetic advance was also detected in both populations. Further analysis indicated that this trait was controlled by several genes associated with additive and complementary gene action in F2 population (Table 4). In contrast with F2-R population that was controlled by several genes with additive gene action only (Table 5). Relationship of this trait with panicle characters revealed a highly significant positive correlation excluding grain initiation length (a highly significant negative correlation) in both populations while similarly no significant with panicle number in F2-R population (positive) and F2 population (negative) (Table 6).

Spikelet number

In the parents, the performance of spikelet number was lower than the distribution of progenies. The different panicle characters between parents generated a F2 population with a wide distribution. For spikelet number character, F2 population mean was above 270 grains per panicle while parents ranged only from 186 to 253 grain per panicle (Table 2). The broad-sense heritability of segregating distributions were estimated as high (0.82 and 0.75), while genetic advance was broad (31.78 and 25.12) in the F2 and F2-R populations respectively (Table 3). Spikelets number was controlled by additive with complementary epistasis gene action (Tables 4 and 5). The correlation analysis revealed a highly significant positive correlation with other panicle traits except for grain initiation length and panicle number in both F2 and F2-R populations (Table 6).

Panicle number

Based on progeny distribution in F2 and F2-R populations, panicle number had a mean value between their parents ranged from 8.27 to 9.03 (Table 2). Similar to all traits that were mentioned above, this panicle character had high broad-sense heritability (0.87 and 0.90), genetic coefficient variation (30.28 and 32.61) and genetic advance (49.59 and 54.43) in F2 and F2-R populations respectively (Table 3). An additive with complementary epistasis gene action was contribute to this character expression in both populations (Tables 4 and 5). However the difference on number of genes controlled was investigated which multiple genes involved in F2 population while a few genes accumulate in F2-R population. Unlike other panicle characters observed, this trait has no significant correlation except with panicle length and panicle axis length in F2 population (Table 6).

Panicle length

The F2 progenies had panicle length means between their parents performance (26.91 and 27.2) (Table 2). A high broad-sense heritability were estimated in F2 (0.55) while moderate in F2-R population (0.33) (Table 3). The genetic advance was medium-high in the F2 (8.20) and medium-low genetic in the F2-R population (3.90) (Table 3). This character showed different performance between populations in F2 generation. The genes controlling this trait were similarly many genes

and duplicate epistasis gene action in both populations (Table 4 and 5). Panicle length had a higly significant positive correlation with all panicle characters observed except grain initiation lenght in both populations and panicle number in the F2-R population (Table 6).

Grain initiation length

To date, there have been no reports about grain initiation length regarding genetic analysis to explain the heredity pattern of this character. This experiment showed that the progenies of F2 and F2-R (2.23 and 2.33) were between their parental means respectively (Table 2). Subsequently the heritability was estimated as low (0.20 and 0.14) in F2 and F2-R populations respectively (Table 3). Genetic advance was not stable in both populations whether high in F2 while low in F2-R population (Table 3). Grain initiation length character was controlled by several genes with additive gene action in both populations (Tables 4 and 5). There was no significant correlation with other traits except primary branches that were a highly significant positive correlation in both populations (Table 6).

Panicle axis length

Panicle axis length had a narrow range (22 and 21.88) in F2 and F2-R populations respectively (Tabel 2). Both populations had high broad-sense heritability (0.73 and 0.58) (Table 3). Nevertheless genetic advance differed between the F2 population (high) and F2-R population (moderate) (Table 3). The gene action of the F2 population was estimated to be additive with complimentary epistasis, while F2-R population had additive with duplicate epistasis (Table 4 and 5). However, both populations were controlled by multiple genes. The correlation study of panicle axis length revealed that a highly significant positive correlation with other characters (Table 6).

Correlation within panicle characters

Relationships of the panicle characters in F2 populations

Correlation analysis of F2 population revealed that most of panicle character had highly significant positive correlation. In contrast, panicle number had no significant correlation with other panicle characters observed except panicle length (0.22) and panicle axis length (0.16). Similarly for a grain initiation length that only had highly significant correlation with primary branch (0.24). Simultaneously, both panicle number and grain initiation length had no significant correlation with primary branches, secondary branches, tertiary branches and spikelet number. Negative correlation was detected between panicle number and tertiary branch (-0.02) as well as tertiary branches and grain initiation length (-0.01) yet there was no significant correlation (Table 6).

Relationship of panicle characters in F2-R population

The F2-R progenies distribution showed that panicle number had no significant correlation with all panicle characters observed. Furthermore, there was a negative correlation between panicle number and grain initiation lenght (-0.03). On the other

hand, grain initiation length only had positively significant correlation with primary branches, whereas negatively significant correlation were estimated in both tertiary branches (-0.16) and spikelet number (-0.17). All panicle characters observed had a highly significant positive correlation among F2-R population except panicle number and grain initiation length (Table 6).

DISCUSSION

Further investigation on panicle morphology of rice are crucial in terms of increasing yield potential. Determining genotypes as either female or male in crossing could cause different results (i.e. performance of progeny). This study revealed that there was no maternal effect for all panicle characters observed in F1 generation. Nevertheless, a wide variation of panicle traits among F2 populations were recorded but there were non statistically significant differences. Surprisingly, some panicle characters come out with unpredicted performance especially for secondary branches, tertiary branches, spikelet number and panicle axis lenght that have mean higher than parents in both F2 and F2-R populations.

This study showed that most panicle characters observed had a high broad-sense heritability in both F2 and F2-R populations. Broad-sense heritability of primary branches, secondary branches, tertiary branches, grain number, panicle number and panicle axis length showed high category in both F2 and F2-R populations. Part of this finding was consistent with results reported by Lestari *et al*. (2015). An opposite finding was for grain initiation length, which showed a low broad-sense heritability in both populations. The differences of heritability estimations were for panicle length character where the F2 population showed high broad-sense heritability, while a moderate heritability was observed in F2-R population. The difference of heritability values for both populations was more affected by environmental factors. High heritability of some traits indicated that these characters could be improved thus grain yield could depend on correlated traits.

A genetic coefficient of variation was estimated that a broad criteria for tertiary branches and panicle number in F2 population. Similar moderate genetic coefficient variation was observed for spikelet number and grain initiation length whether narrow criteria for primary branches, panicle length and panicle axis length in both F2 and F2-R populations. It was known that the size of the inflorescence meristem at the time of branch formation determines number of primary branches because it defines the potential space, which available for branch differentiation (Mu *et al*., 2005). However, Zheng *et al*. (2006) reported that as part of panicle morphology, the primary branch grains are not so effective in increasing the grain numbers per panicle, therefore research has been more focused on the secondary branch grains. Thus, a narrow coefficient genetic variation of primary branches would not be useful to achieve the desirable heavy panicles of rice. The characters with broad genetic coefficient variation could be useful as source material for hybridization in terms of increasing yield. Therefore, the results suggested to focus on tertiary branches, secondary branches and panicle number due to their

genetic variation could improved the performance.

Most of panicle characters indicated high genetic advance especially for secondary and tertiary branches except panicle length in both populations as well as grain initiation length and panicle axis length in F2-R populations. High genetic advance could be useful for efficient selection in future generations. In addition, the importance of secondary branches was also reported that in terms of the breeding of super-high-yield rice, erect panicle types with more superior upper grains in the secondary branches would be the key factors (Jin *et al*., 2010). High genetic advance coupled with high heritability was also exhibited by harvest index, number of spikelets per panicle and spikelet fertility percentage, and therefore selection may be effective for these characters (Bisne *et al*., 2009). Nevertheless, increasing of spikelet number in contrast with panicle population which decreased markedly whether no significant difference in the 1000-grain weight (He *et al*., 2010).

Estimation of number and gene action in both populations showed that primary branches and grain initiation length had additive and multiple gene action while secondary branches and spikelet number had additive with complementary epistasis and multiple gene action in both F2 and F2-R populations. It defined that panicle length was controlled by multiple genes in both populations. Our findings were consistent with previous studies, which showed number of secondary branches had a normal distribution in the F2 population and were controlled by many genes (Jin *et al*., 2010). Number of genes controlling the character will determine the distribution of the character in a population. Besides the contribution from single loci, it has been hypothesized that epistasis is one component of the genetic basis of quantitative traits. Epistasis refers to multi-locus gene interactions that are reflected in the phenotype. The research findings that grain initiation length and number of primary branches has been showed additive gene action. The additive × additive effects can be inherited in rice and selected for (He *et al*., 2010).

This study showed that there was no maternal effect for all panicle characters observed in F1 population. Furthermore, genetic analysis such as number and gene action could be investigated in F2 generation. However, the differences of gene action for some panicle characters in F2 generations are affected by environment factors and interaction of genotype and environment. The differences were observed on number of tertiary branches and panicle axis length that have similar additive gene action in both populations but there was an epistasis effect. The F2 populations reflect the performance (phenotype) of all agronomic traits especially panicle characters. Nevertheless genotype consists of a set of additive, dominant and epistasis genes action. Therefore, the differences of gene action in F2 and F2-R populations also related to epistasis gene action.

This study revealed that spikelet number per panicle had a highly significant positive correlation with panicle length, panicle axis, number of primary branch, secondary branch and tertiary branch. It indicated that panicle size would determine the number of grains per panicle due to wide spacing of grain

distributed along the panicle. Similar findings were also reported by Kato (2004), who revealed that the increasing of number of primary branches per panicle was correlated with an increased number of spikelets on the primary branches. It was also reported previously by Li *et al*. (2014) that panicle number was an important first-order trait that influenced grain yield. Similar results with correlation and distribution analysis of the secondary branch grains on panicle axis manifested that yield was more closely linked with the secondary branches. Thus its valuable genetic characters indicated that secondary branches could be a selection character in rice plant breeding. Spikelets number was most linked with yield, which was determined, chiefly by number of primary and secondary branch (Kobayashi *et al*., 2001). It also can be used as the most reliable selection index for yield improvement in rice since it is the most contributing attribute to yield (Augustina *et al*., 2013; Khatun *et al*., 2015).

This research finding suggested that panicle branching consisted of number of primary, secondary and tertiary branches, which were decisive factors affecting spikelet number, and were highly positively correlated. In agreement with Jin *et al*. (2010), the grain numbers per panicle were primarily determined by the numbers and distribution of secondary branches on the panicle axis. On the other hand, the past study reported that a higher leaf photosynthetic rate and root activity during filling phase, greater biomass accumulation and assimilate transport after heading, as well longer, thicker and more erect upper three leaves were important morphological and physiological traits of high filled-grain number, which could be considered as selection criterion to develop large-panicle varieties (Yao *et al*., 2016).

Correlation coefficient analysis enables the estimation of some characters combination as indicators of certain valuable characters as grain yield. It provides reliable information on selection for simultaneous improvement of desirable yield component characters (Venkanna *et al*., 2014). Panicle length, panicle axis length, primary branches, secondary branches, tertiary branches and spikelet number characters had a highly significant correlation each other except grain initiation length in both F2 and F2-R populations as well panicle length in F2-R population. Most of the panicle characters observed had positive correlations, whereas a negative correlation was detected for only grain initiation length and some traits with panicle number.

Branching in stems of plants (i.e. tillers) was very different and uncorrelated with panicle branching. There was no statistically significant correlation between panicle number related to number of productive tillers with panicle branches. This investigation showed that panicle number had no correlation or relationship with grain initiation length or with other panicle characters observed. Thus panicle number and grain initiation length would be unnecessary characters to study panicle morphology in term of the improvement of rice yield potential. However, the heredity of panicle characters was found to be stable for primary branches, secondary branches, tertiary branches and spikelet number.

CONCLUSION

All panicle characters observed showed high broad-sense heritability for both populations (F1 and F1R) except for grain initiation length (low) and panicle length (moderate). Spikelet number had a highly significant positive correlation with panicle length, panicle axis length, primary branches, secondary branches, and tertiary branches. Based on the genetic analysis in F2 generation, number of secondary and tertiary branches could be the prior character selection in term of developing the heavy panicle. It considered that these characters showed additive gene action, a high heritability and genetic advance and highly significant positive correlation with spikelet number. This study revealed that the panicle branches and spikelet number could be improved simultaneously due to their significant correlation to each character.

ACKNOWLEDGEMENTS

The research was supported by the Ministry of Research, Technology and Higher Education of the Republic of Indonesia in 2016 and 2017 contract number 079/SP2H/LT/DRPM/II/2016 and 011/SP2H/LT/DRPM/IV/2017 to H.A.

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