



## DEVELOPMENT OF RICE GERMPLASM BASED ON GENETIC VARIABILITY IN F<sub>5</sub> SEGREGATING POPULATIONS

W.U. KHAN<sup>1\*</sup>, S.M.A. SHAH<sup>1</sup>, H. ULLAH<sup>2\*</sup>, I.H. KHALIL<sup>1</sup>, S.A. JADOON<sup>1</sup>, and D. WANG<sup>3\*</sup>

<sup>1</sup>Department of Plant Breeding and Genetics, University of Agriculture Peshawar, Pakistan

<sup>2</sup>Department of Agriculture, University of Swabi-Khyber Pakhtunkhwa, Pakistan

<sup>3</sup>College of Life Science, Linyi University, Linyi, Shandong, China

\*Corresponding authors' emails: wasifullah8@yahoo.com, Shabkadar@yahoo.com, dwyandywang@163.com  
 Email addresses of co-authors: mehrpbg@gmail.com, drihkhilil@gmail.com, Sultan@aup.edu.pk

### SUMMARY

Water scarcity is a global dilemma, and rice crop needs plenty of water for optimum growth and yield. In the current climate change scenario, developing a broad-based gene pool of rice to help the crop breeders develop high-yielding cultivars needs dire action. This study assessed the genetic variation among 10 diversified parents and their 15 F<sub>5</sub> populations developed under limited water supply for various morphological traits. Parents and F<sub>5</sub> populations showed significant differences at 5% and 1% for most of the studied maturity and yield traits. F<sub>5</sub> population 'Dokri-Basmati/DR-92' exhibited earliest for days to heading (93) with the highest culm length (85.5 cm). Maximum flag leaf area (34.67 cm<sup>2</sup>) resulted for the F<sub>5</sub> population 'DR-83/NIAB-IRRI-8.' On the other hand, the F<sub>5</sub> population 'DR-83/DR-92' excelled in performance for the number of primary branches panicle<sup>-1</sup> (11). F<sub>5</sub> population 'IR-8/NIAB-IRRI-9' displayed the longest panicle (28.70 cm) with the highest number of secondary branches panicle<sup>-1</sup> (38). Three of the F<sub>5</sub> populations 'DR-92/DR-83,' 'DR-83/NIAB-IRRI-8,' and 'NIAB-IRRI-9/IR-8,' displayed maximum heritability for panicle length (0.82), the number of primary branches (0.80), and secondary branches panicle<sup>-1</sup> (0.94), respectively, offering the prospects for development of potentially high-yielding variety. The highest genetic advance for panicle length (9.87%) emerged from the F<sub>5</sub> population 'DR-92/DR-83,' which also had the highest heritability for this trait. F<sub>5</sub> population 'DR-83/DR-92' manifested maximum genetic advance (3.32%) for primary branches panicle<sup>-1</sup>, while 'NIAB-IRRI-9/IR-8' revealed the highest genetic advance (6.26%) for secondary branches panicle<sup>-1</sup>. Both of these populations may be suitable for developing the spreading type of rice germplasm with the potential water stress. F<sub>5</sub> populations displayed differential responses for the studied traits, with none of the segregating populations excelling for studied maturity and yield traits. However, the germplasm pool created can serve as a better collection for improving existing populations from a production traits perspective under water-stress conditions or developing new cultivars focusing these traits for the target water stress region(s).

**Keywords:** Broad sense heritability, F<sub>5</sub> populations, genetic advance, genetic variations, maturity traits, panicle traits, rice

**Key findings:** The study suggested that several genotypes have the potential for use in a breeding program for abiotic stresses, even if no genotypes showed as best for all the traits because of their diverse background. The germplasm can serve as material in the indigenous breeding program of rice and could also be available to other researchers as per a material transfer agreement for secondary breeding.

Communicating Editor: Prof. Dr. Zahoor Ahmed Soomro

**To cite this manuscript:** Khan WU, Shah SMA, Ullah H, Khalil IH, Jadoon SA, Wang D (2022). Development of rice germplasm based on genetic variability in F<sub>5</sub> segregating populations. *SABRAO J. Breed. Genet.* 54(5): 993-1003. <http://doi.org/10.54910/sabrao2022.54.5.3>.

## INTRODUCTION

Rice belongs to the tribe Oryzeae, the family Poaceae, and the subfamily Pooideae (Iqbal *et al.*, 2018; Chavan *et al.*, 2022). The known cultivated types of rice include *Oryza sativa* L. (Asian rice) and African rice as *Oryza glaberrima* Steud (Semon *et al.*, 2005). Rice is diploid with 24 chromosomes (Chang and Bardenas, 1965). It is one of the most important staple foods in the world (Hanjra and Qureshi, 2010; Sen *et al.*, 2020). On a nutritional basis, most of the cultivated rice provides over 21% of the basic caloric needs to feed half of the human population and 76% of the caloric intake to feed, especially the people of Southeast Asia (Zhao *et al.*, 2020; Singh *et al.*, 2021). Based on kernel color, rice categorizes into two classes, i.e., brown rice and white rice, with storage in both cool and dry areas. The nutritional value of brown rice is commendable compared with that of white rice due to the presence of endosperm, which contains protein, starch, and lipids (Yang *et al.*, 2019).

Globally, rice is grown in 160.2 million ha, producing 755.5 million t (FAOSTAT, 2021). Asia considers the foremost hub of rice growers (90%) and consumers by providing rice as food to half of the world's population (Yugandhar *et al.*, 2018). In Pakistan, planting rice covers an area of 3.03 million ha, with a total production of 7.41 million t. As per the Pakistan Bureau of Statistics, in Punjab province of Pakistan alone, growing rice covers an area of 2.02 million ha, with 4.1 million t of production (PBS, 2020). Similarly, in the Khyber Pakhtunkhwa province, a report has stated an area under rice cultivation covered 0.67 million ha, with 1.58 million t of production (KPBOS, 2020). The grain size of Pakistani rice is longer than that of the rice cultivars of other countries (Siddiqui and Karim, 2007).

For the success of any breeding program, the presence of genetic variation, high heritability, and genetic gain for the desired traits in segregating generations proved imperative in a selected environment (Lee *et al.*, 2015). The analysis of variance (ANOVA) estimates whether the variation for a particular trait is either due to the differences in the genetic makeup of the genotypes or due to the environmental components. On the other hand, heritability is the proportion of

phenotypic variance to genotypic variance (Johnson and Frey, 1967). Estimates of heritability show the interactions of genes in the upcoming generations and thus provide an indispensable part of the response to selection for improvement (Akvaforsk, 2005). Genetic improvement of complex traits could result from selecting, under stressed environments, secondary target traits among the breeding lines focusing on heritabilities and genetic advance (Wang *et al.*, 2013).

There is a direct relationship between heritability and response to selection, which gave rise to the genetic advance (Nithya *et al.*, 2020), an improvement assessment in the mean genotypic value of selected plants over the parental population. The utility of heritability increases when used to measure expected genetic advance, which indicates the degree of expected gain in the obtained character under a particular selection pressure in the target region. Thus, genetic advance serves as an essential selection parameter, which supports breeders in crop improvement programs. The recent research targeted to assess genetic variability, heritability, and genetic advance for maturity and panicle traits in F<sub>5</sub> rice populations to develop a broad-based genetic pool for rice improvement programs. Further, it aimed to identify the desirable F<sub>5</sub> populations for onward use in the local or global rice breeding programs for developing superior rice lines/cultivars.

## MATERIALS AND METHODS

Fifteen F<sub>5</sub> rice populations, along with their 10 parents, planted in randomized complete block design with three replications, ensued at the Plant Breeding and Genetics Research Farm of the University of Agriculture, Peshawar-Pakistan, located between 358' 02" N latitude, 731' 46" E longitude with an altitude of 360 ft (Table 1). Each genotype grown in a two-row plot had a row length of 1.5 m, with row-to-row and plant-to-plant distances kept at 30 and 15 cm, respectively. Raising a preliminary nursery in the first week of June and the transplantation of seedlings into a well-puddled field during the first week of July proceeded, applying proper weeding, weedicides and pesticides, and balanced fertilizer for optimum growth. Water stress consists of physiological stress experienced by a plant as a result of a

**Table 1.** Rice genotypes used in the study.

Name of genotype	Pedigree and origin of the genotype
<b>A. List of parental genotypes</b>	
DR-92	IR8/IET1039-2-4 (RRI, Dokri, Larkana, Sindh-Pakistan)
IR-8	Peta/Dee-gee-woo-gen (IRRI, Philippines)
Dokri-Basmati	Local selection (RRI, Dokri, Larkana, Sindh-Pakistan)
DR-83	IR1833/C4-63 (RRI, Dokri, Larkana, Sindh-Pakistan)
Pakhal	IR36/IR10154-23-3-3//IR9129-209-2-2-1 (ARS, Mansehra, Khyber Pakhtunkhwa, Pakistan)
Kashmir-Basmati	Mutant of Basmati-370 (NIAB, Faisalabad, Pakistan)
Sugdesi	Local selection (RRI, Dokri, Larkana, Sindh-Pakistan)
NIAB-IRRI-8	Mutant of IR-8 (NIAB, Faisalabad, Pakistan)
NIAB-IRRI-9	Mutant of IR6 (NIAB, Faisalabad, Pakistan)
DR-82	BU1/CR-115 (RRI, Dokri, Larkana, Sindh-Pakistan)
<b>B. List of F<sub>5</sub> populations</b>	
Dokri-Basmati/DR-92	Dokri-Basmati × DR-92
Dokri-Basmati/Pakhal	Dokri-Basmati × Pakhal
DR-92/DR-83	DR-92 × DR-83
DR-92/ Dokri-Basmati	DR-92 × Dokri-Basmati
Pakhal/Kashmir-Basmati	Pakhal × Kashmir-Basmati
DR-83/Dokri-Basmati	DR-83 × Dokri-Basmati
DR-83/DR-92	DR-83 × DR-92
DR-83/NIAB-IRRI-8	DR-83 × NIAB-IRRI-8
IR-8/Sugdesi	IR-8 × Sugdesi
DR-83/Sugdesi	DR-83 × Sugdesi
NIAB-IRRI-9/IR-8	NIAB-IRRI-9 × IR-8
IR-8/NIAB-IRRI-9	IR-8 × NIAB-IRRI-9
DR-82/IR-8	DR-82 × IR-8
Dokri-Basmati/DR-83	Dokri-Basmati × DR-83
Dokri-Basmati/Sugdesi	Dokri-Basmati × Sugdesi

ARS: Agricultural Research Station, Dhodial, Mansehra, Pakistan, IRRI: International Rice Research Institute, Laguna, Philippines, NIAB: Nuclear Institute for Agriculture & Biology, Faisalabad, Pakistan, RRI: Rice Research Institute, Dokri, Larkana, Sindh, Pakistan

lack of available moisture. Water stress application continued 40 days after transplantation for two weeks, irrigating the field once during the remaining growing season. Data recording on flag leaf area, days to heading, culm length, days to maturity, panicle length, primary branches panicle<sup>-1</sup>, and secondary branches panicle<sup>-1</sup>, used 10 randomly selected plants of each genotype in each replication.

### Statistical analysis

The compiled data underwent analysis of variance technique as outlined by Singh (1985) for the 10 parents and 15 F<sub>5</sub> rice lines. Also, using the least significant difference (LSD) test separated means for proper comparison. Broad sense heritability ( $h^2_{BS}$ ) computation for each F<sub>5</sub> population separately used the following formula outlined by Mahmud and Kramer (1951).

$$h^2 = \frac{V_{F_5} - \sqrt{V_{P_1} \times V_{P_2}}}{V_{F_5}}$$

Where VF<sub>5</sub> = Variance of F<sub>5</sub> population for a trait; V<sub>p1</sub> and V<sub>p2</sub> = Parental variances of a particular trait. Similarly, the estimation of the expected genetic advance in each cross combination for the studied traits used the following computation of Johnson *et al.* (1955).

$$GA = K \times \sqrt{\sigma^2_p} \times h^2$$

Where GA = Genetic advance; K = 1.76 (10% selection intensity);  $h^2$  = Heritability coefficient, and  $\sqrt{\sigma^2_p}$  = Phenotypic standard deviation, with the genetic advance taken as the percent of the mean using the formula of Falconer and Mackay (1996).

$$GA\% = \frac{GA}{\bar{X}} \times 100$$

Where X is the mean of a particular trait of the F<sub>5</sub> population.

## RESULTS

### Days to 50% heading

Significant ( $P \leq 0.01$ ) differences resulted among the parents and their derived  $F_5$  populations, while parents vs.  $F_5$  populations revealed non-significant ( $P > 0.05$ ) differences for days to heading (Table 2). Mean values for heading ranged from 92.3 to 107.4 days for the parents, with Kashmir-Basmati (92.3) as the early heading genotype and DR-82 (107.4) as the late heading genotype, whereas in  $F_5$  populations, the range for heading days varied from 92.9 to 107.2. Among the  $F_5$  populations, 'Dokri-Basmati/DR-92' gave the earliest (92.9) heading line and 'IR-8/Sugdesi' (107.2) as the late heading. Two  $F_5$  populations, 'DR-82/IR-8' and 'Dokri-Basmati/DR-83,' each headed in 107 days (Table 3). For days to heading, the genetic variance (19.96) was greater in magnitude than that of the environmental variance (7.09) for the tested rice genotypes, with an overall heritability of 0.74 and its value as a percent of the population mean rated at 6.77% (Table 5).

### Flag leaf area

Data regarding flag leaf area exhibited significant differences ( $P \leq 0.01$ ) among parents,  $F_5$  populations, and parents vs.  $F_5$  populations (Table 2). Among parents, the IR-8 showed the maximum flag leaf area (41.6  $\text{cm}^2$ ), whereas, among the  $F_5$  populations, 'DR-83/NIAB-IRRI-8' displayed the highest (34.6  $\text{cm}^2$ ) for flag leaf area and 'Dokri-Basmati/Sugdesi' had the lowest (22.1  $\text{cm}^2$ ) (Table 3). The  $F_5$  population 'DR-83/NIAB-IRRI-8' displayed the estimated highest magnitude of broad sense heritability (0.88), whereas the lowest estimate (0.71) for 'DR-83/Sugdesi.' In a similar pattern, the estimated highest (5.55%) and lowest genetic advance (3.45%) occurred for the  $F_5$  populations 'DR-83/NIAB-IRRI-8' and 'DR-83/Sugdesi,' respectively (Table 6).

### Culm length

The mean square for culm length manifested significant differences ( $P \leq 0.01$ ) among parents,  $F_5$  populations, and parents vs.  $F_5$  populations (Table 2). Mean data regarding culm length between parents varied from 54.9 to 96.6 cm, and the mean value for culm length among  $F_5$  populations ranged between 49.9 and 85.5 cm.  $F_5$  populations, 'Dokri-Basmati/DR-92' and 'Pakhal/Kashmir-Basmati,'

produced the tallest (85.5 cm) plants, whereas  $F_5$  population 'DR-82/IR-8' had the short stature (49.9 cm) plants (Table 3). The highest broad sense heritability (0.85) surfaced for each of the  $F_5$  populations, 'Dokri-Basmati/Sugdesi' and 'Dokri-Basmati/DR-92,' whereas the lowest heritability (0.64) by 'DR-82/IR-8.' Surprisingly, the maximum value (5.62%) of genetic advance emerged for the  $F_5$  population 'Dokri-Basmati/Sugdesi,' which had the highest heritability as well; however, the lowest value of genetic advance (2.93%) came from 'Dokri-Basmati/DR-83' (Table 6).

### Days to maturity

Analysis of variance for days to maturity exhibited highly significant ( $P \leq 0.01$ ) differences among parents, whereas  $F_5$  populations showed significant ( $P \leq 0.05$ ) differences. On the other hand, parents vs.  $F_5$  populations exhibited non-significant ( $P > 0.05$ ) differences (Table 2). Mean values among the parents for maturity ranged from 129.3 to 148 days, and among the  $F_5$  populations, mean data for maturity ranged between 126.2 and 145.8 days.  $F_5$  population, 'Dokri-Basmati/DR-83,' manifested minimum days to maturity (126.2), whereas 'DR-83/Dokri-Basmati' took maximum days of 145.8 to attain physiological maturity (Table 3). Genetic variance (20.49) showed comparatively less than the environmental variance (39.68) for the days to maturity for all the tested genotypes of rice, showing the highest environmental influence factors. The magnitude of heritability for days to maturity was low (0.34), with a genetic advance of 3.41% (Table 5).

### Panicle length

The studied  $F_5$  populations exhibited significant ( $P \leq 0.01$ ) differences in panicle length. Similarly, significant differences ( $P \leq 0.05$ ) also appeared for parental lines, with the parents versus  $F_5$  population effect as non-significant for this particular trait (Table 2). Panicle length among the parents varied between 21.1 and 27.8 cm. Among the  $F_5$  populations, mean values for panicle length ranged from 21.5 to 28.7 cm.  $F_5$  population, 'Dokri-Basmati/DR-92,' produced the shortest panicle (21.5 cm), whereas 'IR-8/NIAB-IRRI-9' manifested the spread-out (28.7 cm) panicle (Table 4). Heritability for panicle length among  $F_5$  populations varied between 0.16 and 0.82, and genetic advances ranged from 1.02 to 9.87. The  $F_5$  population 'DR-92/DR-83' had the

highest heritability magnitude (0.82) and genetic advance (9.87), whereas the F<sub>5</sub> population 'IR-8/Sugdesi' gave the lowest heritability (0.16) with low genetic advance (1.02) (Table 6).

### Primary branches panicle<sup>-1</sup>

Primary branches panicle<sup>-1</sup> exhibited significant ( $P \leq 0.01$ ) differences among the F<sub>5</sub> populations and parents vs. the F<sub>5</sub> populations, with significant differences ( $P \leq 0.05$ ) observed

among the parents (Table 2). Among parents, mean values for primary branches panicle<sup>-1</sup> ranged between 8.3 and 9.6. Maximum primary branches panicle<sup>-1</sup> (9.6) among the parental genotypes resulted from Pakhal. Similarly, mean values among the F<sub>5</sub> populations varied between 8.3 and 11.4. F<sub>5</sub> population, 'DR-83/DR-92,' displayed maximum primary branches panicle<sup>-1</sup> (11.4), whereas minimum primary branches panicle<sup>-1</sup> (8.3) with 'DR-92/DR-83' (Table 4). The magnitude of heritability for primary branches

**Table 2.** Mean squares for various morphological traits in rice genotypes.

Traits	Replications (df=2)	Genotypes (df=24)	Parents(P) (df=9)	F <sub>5</sub> population (F <sub>5</sub> ) (df=14)	P vs. F <sub>5</sub> (df=1)	Error(df=48)
Days to 50% heading	24.9	67.0**	76.1**	64.4**	20.6	7.1
Flag leaf area	10.2	69.1**	82.0**	32.5**	463.7**	5.3
Culm length	5.1	445.7**	475.6**	402.0**	788.8**	9.7
Panicle length	4.4	10.8**	10.5*	11.4**	5.1	4.5
Days to maturity	103.1	101.2**	134.9**	86.6*	2.3	39.7
Primary branches panicle <sup>-1</sup>	0.2	1.3**	0.6*	1.7**	2.8**	0.3
Secondary branches panicle <sup>-1</sup>	4.5	27.4**	17.9*	33.9**	22.4	7.8

\*, \*\* = significant at 5% and 1% level of probability, respectively.

**Table 3.** Mean values of rice genotypes for various morphological traits.

Genotypes	Days to heading	Flag leaf area (cm <sup>2</sup> )	Culm length (cm)	Days to maturity
DR-92	95.5	29.3	83.4	129.3
IR-8	97.9	41.6	62.0	131.5
Dokri-Basmati	95.5	31.9	66.2	134.0
DR-83	99.2	32.3	96.6	144.6
Pakhal	94.0	33.0	82.3	130.4
Kashmir-Basmati	92.3	33.5	87.3	130.3
Sugdesi	104.8	30.9	76.4	137.8
NIAB-IRRI-8	101.0	30.3	54.9	136.8
NIAB-IRRI-9	103.9	36.7	83.2	148.0
DR-82	107.4	21.2	75.9	143.2
Parental means	99.1	32.0	76.8	136.6
LSD <sub>0.05</sub> Parents	4.9	4.2	5.7	11.6
<b>F<sub>5</sub> Populations</b>				
Dokri-Basmati/DR-92	92.9	30.2	85.5	130.1
Dokri-Basmati/Pakhal	97.0	23.6	73.0	139.8
DR-92/DR-83	94.4	23.9	81.1	129.6
DR-92/Dokri-Basmati	99.6	29.1	61.1	138.5
Pakhal/Kashmir-Basmati	99.4	26.8	85.5	138.8
DR-83/Dokri-Basmati	103.7	22.9	70.6	145.8
DR-83/DR-92	100.0	26.0	64.8	135.1
DR-83/NIAB-IRRI-8	102.0	34.6	77.3	135.6
IR-8/Sugdesi	107.2	25.6	78.8	141.1
DR-83/Sugdesi	102.9	29.2	61.6	134.7
NIAB-IRRI-9/IR-8	95.5	25.4	54.3	139.0
IR-8/NIAB-IRRI-9	97.8	29.0	57.6	143.2
DR-82/IR-8	107.0	28.3	49.9	134.2
Dokri-Basmati/DR-83	107.0	27.9	69.6	126.2
Dokri-Basmati/Sugdesi	96.9	22.1	82.2	131.9
F <sub>5</sub> Population means	100.2	27.0	70.2	136.2
LSD <sub>0.05</sub> F <sub>5</sub> Populations	4.6	4.0	5.1	11.0
Genotype means	99.8	29.0	72.8	136.4
LSD <sub>0.05</sub> Genotypes	4.3	3.7	5.1	10.3

**Table 4.** Mean values of rice genotypes for various morphological traits.

Genotypes	Panicle length (cm)	Primary branches panicle <sup>-1</sup>	Secondary branches panicle <sup>-1</sup>
DR-92	21.1	9.3	27.7
IR-8	24.9	8.7	31.5
Dokri-Basmati	26.5	8.9	28.7
DR-83	25.8	8.4	27.7
Pakhal	27.8	9.6	31.9
Kashmir-Basmati	27.1	8.4	28.4
Sugdesi	24.3	8.3	32.3
NIAB-IRRI-8	24.5	9.2	30.7
NIAB-IRRI-9	24.8	8.5	32.1
DR-82	26.1	9.2	25.0
Parental means	25.3	8.8	29.6
LSD <sub>0.05</sub> Parents	3.9	0.9	5.1
<b>F<sub>5</sub> Populations</b>			
Dokri-Basmati/DR-92	21.5	8.8	30.7
Dokri-Basmati/Pakhal	24.7	8.5	25.7
DR-92/DR-83	25.6	8.3	30.8
DR-92/Dokri-Basmati	24.4	9.8	34.0
Pakhal/Kashmir-Basmati	24.2	9.4	32.9
DR-83/Dokri-Basmati	25.3	9.4	30.8
DR-83/DR-92	26.1	11.4	34.3
DR-83/NIAB-IRRI-8	27.6	9.2	28.3
IR-8/Sugdesi	26.4	8.8	26.3
DR-83/Sugdesi	24.1	9.2	33.2
NIAB-IRRI-9/IR-8	23.1	9.2	28.9
IR-8/NIAB-IRRI-9	28.7	8.6	38.3
DR-82/IR-8	22.4	8.8	29.3
Dokri-Basmati/DR-83	23.9	9.1	28.1
Dokri-Basmati/Sugdesi	21.8	9.9	29.2
F <sub>5</sub> Population means	24.8	9.1	30.5
LSD <sub>0.05</sub> F <sub>5</sub> Populations	3.7	0.9	4.8
Genotype means	25.0	9.0	30.3
LSD <sub>0.05</sub> Genotypes	3.4	0.8	4.5

**Table 5.** Genetic parameters for various morphological traits in rice genotypes.

Traits	Ve	Vg	Vp	$h^2_{BS}$	GA (%)
Days to 50% heading	7.09	19.96	27.06	0.74	6.77
Days to 50% maturity	39.68	20.49	60.17	0.34	3.41

panicle<sup>-1</sup> among the F<sub>5</sub> populations ranged between 0.64 and 0.80, while genetic advance for primary branches panicle<sup>-1</sup> varied from 1.80 to 3.32. Among the F<sub>5</sub> populations, 'IR-8/Sugdesi' displayed the lowest heritability (0.64) and a low genetic advance of 1.80 units, whereas F<sub>5</sub> populations, 'DR-83/DR-92' and 'DR-83/NIAB-IRRI-8' manifested high heritability (0.80), respectively. However, 'DR-83/DR-92' recorded the highest value of genetic advance (Table 6).

### Secondary branches panicle<sup>-1</sup>

Analysis of variance regarding secondary branches panicle<sup>-1</sup> displayed significant ( $P \leq 0.01$ ) differences for F<sub>5</sub> populations, with significant ( $P \leq 0.05$ ) differences shown by parents. Parents versus F<sub>5</sub> populations displayed non-significant differences for this particular trait (Table 2). Mean values for

secondary branches panicle<sup>-1</sup> among the parents ranged between 25 and 32.3. Among the F<sub>5</sub> populations, mean values for secondary branches panicle<sup>-1</sup> varied from 25.7 to 38.3. F<sub>5</sub> population, 'Dokri-Basmati/Pakhal,' manifested the least secondary branches panicle<sup>-1</sup> (25.7), whereas the maximum secondary branches panicle<sup>-1</sup> (38.3) resulted from the F<sub>5</sub> population, 'IR-8/NIAB-IRRI-9' (Table 4). Estimates of broad sense heritability for the secondary branches panicle<sup>-1</sup> among the F<sub>5</sub> populations ranged from 0.69 to 0.94, whereas genetic advance varied from 2.62 to 6.26 (Table 6). F<sub>5</sub> population, 'NIAB-IRRI-9/IR-8,' had the maximum values of broad sense heritability (0.94) with the highest genetic advance of 6.26 units. Inversely, the lowest heritability (0.69) with low genetic advance (2.62) emerged for 'Dokri-Basmati/DR-92' (Table 6).

**Table 6.** Heritability ( $h^2_{BS}$ ) and genetic advance as percent of the mean (GA) for flag leaf area, culm length, panicle length, and primary branches panicle<sup>-1</sup> in F<sub>5</sub> rice populations.

F <sub>5</sub> populations	Flag leaf area		Culm length		Panicle length		Primary branches panicle <sup>-1</sup>		Secondary branches panicle <sup>-1</sup>	
	$h^2_{BS}$	GA	$h^2_{BS}$	GA	$h^2_{BS}$	GA	$h^2_{BS}$	GA	$h^2_{BS}$	GA
Dokri-Basmati/DR-92	0.84	4.87	0.85	5.05	0.57	5.76	0.74	2.50	0.69	2.62
Dokri-Basmati/Pakhal	0.77	3.72	0.80	4.46	0.54	5.24	0.74	2.35	0.93	5.14
DR-92/DR-83	0.80	4.19	0.69	3.31	0.82	9.87	0.78	3.09	0.87	4.53
DR-92/Dokri-Basmati	0.81	4.35	0.76	3.76	0.23	1.47	0.71	2.40	0.85	4.71
Pakhal/Kashmir-Basmati	0.78	3.84	0.81	5.09	0.59	4.33	0.73	2.29	0.90	4.52
DR-83/Dokri-Basmati	0.79	4.37	0.77	4.21	0.29	2.17	0.76	2.59	0.83	3.57
DR-83/DR-92	0.74	3.47	0.80	4.78	0.55	3.97	0.80	3.32	0.81	3.80
DR-83/NIAB-IRRI-8	0.88	5.55	0.72	3.78	0.30	1.77	0.80	2.81	0.89	4.75
IR-8/Sugdesi	0.74	4.02	0.79	4.64	0.16	1.02	0.64	1.80	0.88	4.47
DR-83/Sugdesi	0.71	3.45	0.75	3.93	0.43	3.02	0.71	2.33	0.89	4.84
NIAB-IRRI-9/IR-8	0.82	4.79	0.70	3.58	0.26	1.93	0.73	2.61	0.94	6.26
IR-8/NIAB-IRRI-9	0.79	4.29	0.76	4.42	0.52	4.69	0.73	2.53	0.89	4.55
DR-82/IR-8	0.75	3.88	0.64	3.13	0.30	2.58	0.73	2.67	0.86	4.16
Dokri-Basmati/DR-83	0.77	3.90	0.65	2.93	0.51	6.41	0.71	2.27	0.83	3.81
Dokri-Basmati/Sugdesi	0.83	5.02	0.85	5.62	0.56	3.87	0.77	2.81	0.90	5.25

## DISCUSSION

The early heading values as one of the desirable features in rice crops, serving as a principal character in most of the plant breeding programs, as it provides sufficient time for grain formation. Enhanced grain filling duration, in turn, increases the grain weight (Sattar, 2010). The variation in the parents and F<sub>5</sub> populations for heading days was due to the genetic pool and diversified origin of the parents, with the environment affecting these crosses. Study results align with the findings of Bitew (2016); Kishore *et al.* (2018); Ganapati *et al.* (2020); and Dev *et al.* (2022). The observed high heritability and genetic advance for days to heading of the study agree with an earlier report by Bekele *et al.* (2013). It said the evaluated 64 rice genotypes in field conditions exhibited high heritability and genetic advance. Similarly, a recent report on high heritability with moderate genetic advance came out (Gupta *et al.*, 2022) for a set of rice lines.

Photosynthesis depends on several active leaves and expanded flag leaf area as it plays a prominent role in determining the yield potential of cereal crops. Flag leaf is responsible for producing more than 70% of the photo-assimilates directly absorbed by the grains, ultimately contributing toward the final yield (Yang *et al.*, 2006). Significant ( $P \leq 0.01$ ) genetic variation observed among the rice genotypes, parents, F<sub>5</sub> populations, and parents vs. F<sub>5</sub> populations for flag leaf area paralleled with the findings reported previously

for flag leaf area in rice populations (Bhadru *et al.*, 2012; Hefena *et al.*, 2016; Longkho *et al.*, 2020; Pushkarnath *et al.*, 2022). The highest magnitude of heritability (>80%) coupled with genetic advance of 5.55 units estimated for the F<sub>5</sub> population, 'DR-83/NIAB-IRRI-8' has the potential use for the improvement of a specific trait or the development of cultivars for water-limited regions. High heritability and genetic advance for flag leaf guarantee the development of high-yielding bold-grain rice genotypes for stressed environments (Devi *et al.*, 2016; Srujana *et al.*, 2017; Sumanth *et al.*, 2017).

Increased culm length enhances rice resistance to lodging along with maximum grain yield. The mean square for the culm length in this study showed significant ( $P \leq 0.01$ ) genetic variations among parental rice genotypes, F<sub>5</sub> populations, and parents vs. F<sub>5</sub> populations, which are in agreement with the findings of Iqbal *et al.* (2018). The authors reported significant ( $P \leq 0.01$ ) differences for culm length in 38 rice lines for yield and yield-associated traits. Similarly, Lingaiah *et al.* (2015) also reported significant genetic variations for culm length while testing a set of 31 rice genotypes. Broad sense heritability and elevated genetic advance confirm the findings of the previously reported study in cereals (Jawad *et al.*, 2013; Shrivastava *et al.*, 2014) for culm length.

The best strategy to develop and screen the population is appropriately grouping the available germplasm based on physiological maturity. Early maturity is a

desirable parameter for plant breeders to screen genotypes adaptable to different environments and geographical regions in the current climatic conditions and to categorize them for stressful environments. Significant ( $P \leq 0.01$ ) differences were observed among the parents and derived  $F_5$  populations ( $P \leq 0.05$ ) for days to maturity. Yadav *et al.* (2022) evaluated 72 rice genotypes, including prominent checks, and observed significant ( $P \leq 0.01$ ) differences among them for days to maturity. Likewise, Girma *et al.* (2018) assessed 64 rice genotypes and observed significant ( $P \leq 0.01$ ) differences for the said trait. The consistency for variation was due to the diverse background of the selected parents. On the contrary, Padmaja *et al.* (2008) studied 52 rice genotypes and the variation for maturity days observed was significant at 5% only. High heritability coupled with a high genetic advance in most of the  $F_5$  rice populations matches the result of Bitew *et al.* (2016) for days to maturity.

Likewise, maturity, culm length, leaf area, heading, and panicle length comprise the key parameters for developing high-yielding rice cultivars that influence grain yield (Rashmi *et al.*, 2017; Zheng *et al.*, 2022). Significant ( $P \leq 0.01$ ) differences occurred for the  $F_5$  populations, whereas parental lines showed significantly different for panicle length at 5% only. The non-detrimental variation in parents is because of the fixation of genes that took place with time. Moreover, the parents versus  $F_5$  population effect were non-significant. Previous studies suggest significant differences ( $P \leq 0.01$ ) among the tested genotypes of rice for panicle length (Khaire *et al.*, 2017; Chavan *et al.*, 2022; Yadav *et al.*, 2022). The non-significant differences observed in the  $F_5$  populations confirm that genes responsible for panicle length, especially in the derived lines, deviated from parents with little room for gene fixation. It shows no significant variation resulted in the  $F_5$  populations for panicle length. In this study, some populations gave low (0.16–0.30) or moderate (0.43–0.59) heritability, and just a few lines had high heritability ( $>0.80$ ).  $F_5$  population, 'DR-92/DR-83,' had the highest magnitude of heritability (0.82) and genetic advance (9.87), whereas the lowest heritability (0.16) associated with low genetic advance (1.02) resulted with 'IR-8/Sugdesi'. Other researchers have also reported this wide range of variation for the estimates of heritabilities and genetic advances (Bacha *et al.*, 2015; Gampala *et al.*, 2015; Sarwar *et al.*, 2015; Kahani and Hittalmani, 2016). Moreover, a study reported a broad

range of variation for heritability comprising 26 rice cultivars for yield traits (Ketan and Sarkar, 2014). This wide variation helps the breeder the opportunity to study the trait further and identify the genes responsible for controlling the expression of this trait, as it has shown a strong association with grain yield (Sanghera *et al.*, 2013).

Primary and secondary branches directly contribute to the final yield, with the breeders giving them weight for their associations with grain yield (Singh *et al.*, 2022). The current study observed significant ( $P \leq 0.01$ ) variation among the  $F_5$  populations for primary and secondary branches. However, this variation was found relevant at a 5% probability level for the parental combinations. Furthermore, some genes might have strongly merged, not allowing the parents vs.  $F_5$  populations for notable variation. Iqbal *et al.* (2018) reported significant ( $P \leq 0.01$ ) variability among  $F_{5:6}$  rice populations for primary branches panicle<sup>-1</sup>, as well as, secondary branches panicle<sup>-1</sup>. Observed heritability for almost all  $F_5$  populations resulted in low to high genetic advances. Previous studies suggest that primary branches and secondary branches panicle<sup>-1</sup> have been under the control of genetic influence and high heritability coupled with high genetic advance and could be more suitable for making an indirect selection for grain yield improvement (Sarma *et al.*, 2022; Singh *et al.*, 2022).

## CONCLUSIONS

Developing superior germplasm to derive desirable crop cultivars requires genetic diversity for the desired maturity and yield traits in segregating populations. Significant differences observed among the  $F_5$  populations resulted for the studied maturity and yield traits. However, the studied populations displayed differential potential for various traits on account of diverse genetic backgrounds of parental material used in the crosses. Furthermore, 'IR-8/NIAB-IRRI-9' excelled in performance for panicle length and secondary branches. High broad sense heritability for panicle length, primary and secondary branches were manifested by 'DR-92/DR-83,' 'DR-83/DR-92,' and 'NIAB-IRRI-9/IR-8,' respectively.  $F_5$  population 'DR-92/DR-83' was good for most of the traits as a direct or reciprocal cross. This cross also displayed high genetic advance for panicle length and primary branches.  $F_5$  population 'NIAB-IRRI-9/IR-8' exhibited the maximum genetic advance for



secondary branches panicle<sup>-1</sup>. Based on performance for maturity and other related traits, 'Dokri-Basmati/DR-92,' 'DR-83/DR-92,' and 'NIAB-IRRI-9/IR-8' displayed superiority over their parental lines and thus recommended for future in-depth research, primary and secondary breeding in local and international rice breeding programs.

## ACKNOWLEDGMENTS

The authors confirm their contribution to the paper as follows: provision of the genetic materials, guidance by Shah SMA; study conception and design: Khalil IH; data collection, execution by Khan WU; analysis and interpretation of results by Jadoon SA; draft manuscript preparation and revision by Ullah H and Wang D. All authors reviewed the results and approved the final version of the manuscript.

## REFERENCES

- Akvaforsk Å (2005). Selection and Breeding Programs in Aquaculture. T Gjedrem (ed.). Dordrecht, The Netherlands: Springer, pp. 89-111.
- Bacha QU, Shah SMA, Khalil IA, Muhammad A, Azam SM (2015) Heritability, genetic advance, genotypic and phenotypic correlation studies for yield and yield related traits in F<sub>2</sub> segregating populations of rice (*Oryza sativa*). *Eur. Acad. Res.* 3(1): 1059-1078.
- Bekele BD, Rakhi S, Naveen GK, Kundur PJ, Shashidhar HE (2013). Estimation of genetic variability and correlation studies for grain zinc concentrations and yield related traits in selected rice (*Oryza sativa* L.) genotypes. *Asian J. Exp. Biol. Sci.* 4(3): 345-351.
- Bhadru D, Krishna L, Pasha M, Naik RB (2012). Effect of environment on genetic parameters of hybrid rice. *Int. J. Appl. Biol. Pharm. Tech.* 3(2): 183-187.
- Bitew JM (2016). Estimation of genetic parameters, heritability, and genetic advance for yield related traits in upland rice (*Oryza sativa* L. and *Oryza glaberrima* Steud) genotypes in Northwestern Ethiopia. *World Sci. News* 2(47): 340-350.
- Bureau of Statistics, Khyber Pakhtunkhwa (KPBOS) (2020). Crop Reporting Services, available online at <http://kpbos.gov.pk/> (accessed 21 July 2022).
- Chang TT, Bardenas EA (1965). The morphology and varietal characteristics of the rice plant. *IRRI Tech. Bull.* 4:1-40.
- Chavan BR, Dalvi VV, Kunkerkar RL, Mane AV, Gokhale NB (2022). Studies on genetic variability for yield and yield contributing traits in aromatic rice (*Oryza sativa* L.). *The PharmaInnov. J.* 11(2): 1732-1735.
- Dev A, Dwivedi DK, Kumar A, Singh K, Khan NA, Komal KM, Prasad S, Kumar A (2022). Studies on variability, heritability, and genetic advance for quantitative characters in rice (*Oryza sativa* L.) germplasm. *The PharmaInnov. J.* 11(7): 1698-1701.
- Devi KR, Parimala K, Venkanna V, Lingaiah N, Hari Y, Chandra BS (2016). Estimation of variability for grain yield and quality traits in rice (*Oryza sativa* L.). *Int. J. Pure Appl. Biosci.* 4(2): 250-255.
- Falconer DS, Mackay FC (1996). Introduction to Quantitative Genetics. (4<sup>th</sup> Edition, p. 464) Logman Group Ltd., London, UK.
- FAOSTAT (2021). Production Indices, FAO (data set). <http://www.fao.org/faostat/en/#data/QI> (last access: August 2021).
- Gampala S, Singh VJ, Pathak SK, Srivastava N, Kaushik SK, Rangare NR (2015). Estimation of genetic variability for yield and quality traits in rice (*Oryza sativa* L.) genotypes. *Environ. Ecol.* 33(1A): 303-305.
- Ganapati RK, Rasul MG, Sarker U, Singh A, Faruquee M (2020). Gene action of yield and yield contributing traits of submergence tolerant rice (*Oryza sativa* L.) in Bangladesh. *Bull. Nat. Res. Centre* 44(1): 1-7.
- Girma BT, Kitil MA, Banje DG, Biru HM, Serbessa TB (2018). Genetic variability study of yield and yield related traits in rice (*Oryza sativa* L.) genotypes. *Adv. Crop Sci. Tech.* 6(4): 1000381.
- Gupta H, Purushottam GY, Yadav SK, Singh S, Kumar S (2022). Genetic variability, heritability, and genetic advance for yield and its related traits in rainfed upland rice (*Oryza sativa* L.) genotypes. *The PharmaInnov. J.* 11(2): 2520-2524.
- Hanjra MA, Qureshi ME (2010). Global water crisis and future food security in an era of climate change. *Food Policy* 35(5): 365-377.
- Hefena AG, Sultan MS, Abdel-Moneam MA, Hammoud SA, Barutçular C, El-Sabagh A (2016). Genetic variability, heritability, and genetic advance for yield and associated traits in F<sub>2</sub> rice population. *J. Agric. Biotechnol.* 1(2): 49-58.
- Iqbal A, Shah SMA, Rahman H, Aman F, Rahman A (2018). Genetic variability, heritability and genetic advance for morphological traits in F<sub>5</sub>:6 rice lines. *Sarhad J. Agric.* 34(4): 888-895.
- Jawad R, Fareeha A, Ihsan K (2013). Estimation of heritability for some polygenic traits in hexaploid wheat (*Triticum aestivum* L.). *Int. J. Agric. Crop Sci.* 6(8): 458-463.
- Johnson GR, Frey KJ (1967). Heritabilities of quantitative attributes of oats (*Avena sp.*) at varying levels of environmental stress. *Crop Sci.* 7(1): 43-46.
- Johnson HW, Robinson HF, Comstock RE (1955). Genotypic and phenotypic correlations in soybeans and their implications in selection. *Agron. J.* 47(10): 477-483.

- Kahani F, Hittalmani S (2016). Identification of F<sub>2</sub> and F<sub>3</sub> segregants of 15 rice crosses suitable for cultivation under aerobic situations. *SABRAO J. Breed. Genet.* 48(2): 219-229.
- Ketan R, Sarkar G (2014). Studies on variability, heritability, genetic advance and path analysis in some indigenous Aman rice (*Oryza sativa* L.). *J. Crop. Weed.* 10(2): 308-315.
- Khaire AR, Kunkerkar RL, Thorat BS, Gavai MP, Bhawe SG (2017). Studies on genetic variability for yield and yield contributing traits in local rice (*Oryza sativa* L.). *J. Pharm. Phytochem.* 6(5): 1376-1378.
- Kishore C, Kumar A, Pal AK, Kumar V, Prasad BD, Kumar A (2018). Character association and path analysis for yield components in traditional rice (*Oryza sativa* L.) genotypes. *Int. J. Curr. Microbiol. Appl. Sci.* 7(3): 283-291.
- Lee J, Chin JH, Ahn SN, Koh HJ (2015). Brief history and perspectives on plant breeding. In *Current Technologies in Plant Molecular Breeding* (pp. 1-14). Springer, Dordrecht.
- Lingaiah N, Venkanna V, Cheralu C (2015). Genetic variability, heritability, and genetic advance in rice (*Oryza sativa* L.). *Asian J. Environ. Sci.* 46(4): 917-919.
- Longkho K, Kole PC, Behera PP (2020). Genetic parameter studies in F<sub>4</sub> segregating generation of rice. *J. Pharmacog. Phytochem.* 9(1): 1647-1651.
- Mahmud I, Kramer HH (1951). Segregation for yield, height, and maturity following a soybean cross. *Agron. J.* 43: 605-606.
- Nithya N, Beena R, Stephen R, Abida PS, Jayalekshmi VG, Viji MM, Manju RV (2020). Genetic variability, heritability, correlation coefficient and path analysis of morpho-physiological and yield related traits of rice under drought stress. *Chem. Sci. Rev. Letters* 9(33): 48-54.
- Padmaja D, Radhika K, Rao LV, Padma V (2008). Studies on variability, heritability, and genetic advance for quantitative characters in rice (*Oryza sativa* L.). *Indian J. Plant Genet. Resour.* 21(3): 196-198.
- PBS (2019-2020). Pakistan Bureau of Statistics (PBS), Economic Survey of Pakistan, Ministry of Finance, Government of Pakistan.
- Pushkarnath KM, Reddy AJ, Lal GM, Lavanya GR (2022). Direct and indirect effects of yield contributing characters on grain yield in rice (*Oryza sativa* L.). *Int. J. Pharm. Pharm. Sci.* 34(21): 769-778.
- Rashmi D, Saha S, Loitongbam B, Singh S, Singh PK (2017). Genetic variability study for yield and yield components in rice (*Oryza sativa* L.). *Int. J. Agric. Environ. Biotechnol.* 10(2): 171-176.
- Sanghera GS, Kashyap SC, Parray GA (2013). Genetic variation for grain yield and related traits in temperate red rice (*Oryza sativa* L.) ecotypes. *Not. Sci. Biol.* 5(3): 400-406.
- Sarma MK, Ahmed AN, Saharia DD, Nath MP, Talukdar J, Devi NS, Deka SD, Zaman S, Bhuyan J (2022). Pattern of genetic diversity in indigenous Ahu rice germplasm of Assam. *Electr. J. Plant Breed.* 13(1): 21-27.
- Sarwar G, Hossain MS, Rashid MH, Parveen S (2015). Assessment of genetic variability for agro-morphological important traits in Aman rice (*Oryza Sativa* L.). *Int. J. Appl. Sci. Biotechnol.* 3(1): 73-79.
- Sattar A (2010). Heritability estimates in F<sub>2</sub> populations for various traits in bread wheat. MSc (Hons.) Dissertation submitted to the Department of Plant Breeding and Genetics, University of Agriculture, Peshawar, Pakistan, pp. 39.
- Semon M, Nielsen R, Jones MP, McCouch SR (2005). The population structure of African cultivated rice *Oryza glaberrima* (Steud.) evidence for elevated levels of linkage disequilibrium caused by admixture with *O. sativa* and ecological adaptation. *Genetics* 169(3): 1639-1647.
- Sen S, Chakraborty R, Kalita P (2020). Rice-not just a staple food: A comprehensive review on its phytochemicals and therapeutic potential. *Trends in Food Sci. Technol.* 97: 265-285.
- Shrivastava A, Mishra DK, Koutu GK, Singh SK (2014). Heritability and genetic advance estimation from parental lines of hybrid rice. *Int. J. Sci. Res.* 3(7): 11-13.
- Siddiqui FU, Karim MS (2007). Crop production sustainability with a global perspective. MSc thesis. Environmental System Analysis, Energy and Environment, Chalmers University of Technology, Göteborg, Sweden.
- Singh G, Gupta MK, Chaurasiya S, Sharma VS, Pimenov DY (2021). Rice straw burning: A review on its global prevalence and the sustainable alternatives for its effective mitigation. *Environ. Sci. Pollut. Res.* 28(25): 32125-32155.
- Singh VK, Wahi N, Mishra SK, Singh BD, Singh NK (2022). Studies on genetic variability, correlation analysis, character association, and path analysis of phenotypic characteristics of 12 mega varieties of rice and its near-isogenic lines carrying high grain number per panicle QTL qGN4.1. *Curr. Trends in Biotechnol. Pharm.* 16(1): 35-45.
- Singh RK (1985). Biometrical Methods in Quantitative Genetic Analysis. *Revised Edition*. Kalyani Pub. Ludhiana. New Delhi, India. pp. 318.
- Srujana G, Suresh BG, Lavanya GR, Ram BJ, Sumanth V (2017). Studies on genetic variability, heritability, and genetic advance for yield and quality components in rice (*Oryza sativa* L.). *J. Pharmacog. Phytochem.* 6(4): 564-566.
- Sumanth V, Suresh BG, Ram BJ, Srujana G (2017). Estimation of genetic variability, heritability and genetic advance for grain yield

- components in rice (*Oryza sativa* L.). *J. Pharmacog. Phytochem.* 6(4): 1437-1439.
- Wang Y, Zhang A, Nafisah L, Zhu L, Xu J, Li Z (2013). Selection efficiencies for improving drought/salt tolerances and yield using introgression breeding in rice (*Oryza sativa* L.). *The Crop J.* 1(2): 134-142.
- Yadav G, Vimal SC, Gupta H, Yadav SK, Tiwari AP, Kumar S (2022). Studies on genetic variability, heritability, and genetic advance for yield and its contributing traits in rice (*Oryza sativa* L.) germplasm. *The PharmaInnov. J.* 11(6): 1358-1362.
- Yang X, Chen X, Ge Q, Li B, Tong Y, Zhang A, Li Z, Kuang T, Lu C (2006). Tolerance of photosynthesis to photoinhibition, high temperature and drought stress in flag leaves of wheat: A comparison between a hybridization line and its parents grown under field conditions. *Plant Sci.* 171(3): 389-397.
- Yang Y, Guo M, Sun S, Zou Y, Yin S, Liu Y, Tang S, Gu M, Yang Z, Yan C (2019). Natural variation of OsGluA2 is involved in grain protein content regulation in rice. *Nat. Comm.* 10(1): 1-12.
- Yugandhar P, Sun Y, Liu L, Negi M, Nallamothe V, Sun S, Neelamraju S, Rai V, Jain A (2018). Characterization of the loss-of-function mutant NH101 for yield under phosphate deficiency from EMS-induced mutants of rice variety Nagina22. *Plant Physiol. Biochem.* 130: 1-13.
- Zhao M, Lin Y, Chen H (2020). Improving the nutritional quality of rice for human health. *Theor. Appl. Genet.* 133(5): 1397-1413.
- Zheng H, Sun S, Bai L, Jiang S, Ding G, Wang T, Zhao H, Wang J, Liu H, Yang L, Jia Y (2022). Identification of candidate genes for panicle length in *Oryza sativa* L. ssp. japonica via genome-wide association study and linkage mapping. *Euphytica* 218(2): 1-12.