



Inheritance of some flag leaf and yield characteristics by half-diallel analysis in rice crops (*Oryza Sativa* L.)

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Abstract

This study was conducted during 2018 and 2019 at the Rice Research and Training Centre farm, Sakha, Kafr el Sheikh, Egypt. Six genotypes of rice, Sakha 101, Giza 178, Irat 170, Wab-56-104, IR65500-127 and IR69853 were half-diallel crossed to estimate the combining ability effect as well as sink and yield potential in rice. Sink capacity (number of spikelets/panicle and 1000-grain weight), source leaf (flag leaf length, flag leaf width and flag leaf area), source-sink association (number of spikelets/panicle to flag leaf area ratio) and traits of yield components (filled grains number/panicle and panicle number) plant and grain yield/plant) were analysed. The results indicated that both general and specific combining ability were highly significant for all the studied characteristics. IR65500-127, Giza 178, and Sakha 101 were identified as good parents, so these parents were suggested for a further recombinant breeding programme. The cross of 3 × 5 was found to be superior for flag leaf width and grain yield, while the cross of 1 × 4 was found to be superior for flag leaf length, flag leaf length/width ratio, chlorophyll content and number of panicles/plant. Advancing these crosses and effected selections in segregating generation would be helpful to develop high yielding varieties. The genetic parameter showed a dominant deviation in one direction was controlled for all characters except flag leaf length. The analysis of the regression line showed that the over-dominance played an important role in the inheritance of gene action for grain yield/plant.

Keywords Rice · Diallel · Leaf area · Yield and genetic parameters

Introduction

Rice is the second most common cereal crop in the world; it provides staple food for nearly half of the world's population (Shang et al. 2020). The application of new alternatives in rice breeding is a prospective possibility to release competitive genotypes in comparison with traditional ones (Pauk et al. 2009). Nevertheless, traditional breeding methods still provide the possibility of the development of rice hybrids. Diallel cross technique is one of the different methods of assessing the nature of the gene action of parents. It estimates the combining ability of parents, gene effects, and heterotic effects (Fasahat et al. 2016). Parental lines and their hybrids can be assessed through diallel analysis

in all possible combinations. The general combining ability (GCA) and specific combining ability (SCA) analyses aid to know the excellent parents for using in breeding programmes or to know the promising cross-combinations for cultivar improvement (Acquaah 2007). Diallel analysis can be used to improve the breeding populations or to identify both GCA and SCA effects (Rahimi et al. 2010). GCA is attributed to the effects of additive genes and additive × additives. On the other hand, SCA attributed to non-additive gene action may be the result of dominance and additive × dominant epistasis (Bagheri 2010). Among the different types of diallel crosses, half-diallel hybridization including one directional crosses, makes overall layout more manageable for breeders compared to a doubled number of reciprocal crosses with full diallel analysis (Christie and Shattuck 2010). Heritability estimation aids plant breeders to foretell the achieving generation, to make suitable selection and to assess the quantity of genetic improvement through selection (Khatun et al. 2015). Flag leaf is the main organ for photosynthesis, and it provides the main source of assimilation required for plant growth and panicle development (Tian et al. 2015). The size

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of the flag leaf in rice is also related to the weight of a thousand grains, the weight of the grains per panicle, and other characteristics related to yield (Wang et al. 2020). The grain yield in rice is positively related to the estimated flag leaf size by length, width, area, and flag leaf length to width. Depending on this, improving the traits of flag leaves brings about a high increase in the grain yield (Rahman et al. 2014). The yield of the grains depends on the source, the sink and their relationship. The numbers of spikelets per panicle and grain size are the primary sinks which the photosynthetic product accumulates. The top leaves, especially the flag leaf, are often the most important primary source for the assimilating of the grain yield. These leaf traits are crucial factors in determining the type of plant desired (Tsukaya 2006). The main objectives of this study are to determine combining ability, gene action, broad and narrow sense heritability and inbreeding depression to understand the genetic behaviour of flag leaf and the yield characteristics of some rice progenies through the 6 × 6 genetic variance component.

Materials and methods

Six local and exotic rice varieties represented in Table 1 were provided from the Rice Research and Training Centre's genetic stock. These cultivars were grown during the 2018 planting season at three planting dates with 15 days interval to overcome the differences in their heading time. At heading, these genotypes were crossed in a half-diallel genetic design according to the method of Griffing (1956a, b). This has resulted in 15 direct crosses. The six parents along with the 15 crosses were grown in a complete randomized block design experiment with three replications during the 2019 season. In both seasons, each replicate contained three rows for each parent and cross. Plants were individually transplanted at 20 × 20 cm spacing between seedlings and rows. All recommended agricultural practices and fertilizers were done. Flag leaf width (cm) and flag leaf length (cm) were measured on the main stem of five uniform plants of each cultivar. Flag leaf area (cm²) was calculated in the whole

Table 1 Origin and parentage of the six genotypes used as parents under this study

No	Genotype	Parentage	Origin
1	Sakha 101	Giza 176 × Milyang 79	Egypt
2	Giza 178	Giza 175/Milyang 49	Egypt
3	Irat 170	Not available	Ivory
4	Wab-56-104	IDSA 6/IAC 164	Warda
5	IR65500-127	Not available	IRRI
6	IR69853	Not available	IRRI

IRRI International Rice Research Institute

flowering period following the formulation announced by Yoshida et al. (1976) as follows:

$$\text{Flag leaf area (cm}^2\text{)} = K \times \text{leaf length (cm)} \times \text{maximum width (cm)}$$

where K (0.75) a rectification factor that can be used for the whole growth period, except for the seedling and maturity periods. In addition, panicles number per plant, sink capacity (total spikelets number per panicle and 1000-grain weight), source leaf (flag leaf length, flag leaf width and flag leaf area), source–sink relationship (total spikelets number to flag leaf area ratio and filled grains number per panicle) were estimated.

The studied parents were selected based on the significance of the studied characters and using the analysis of variance with three sources of variance, replicates, genotype and error and were conducted according to Singh and Chaudhary (1985). Analysis of variance was subjected to Randomized Complete Block Design (RCBD) according to Snedecor and Cochran (1989). Data obtained from the 15 F_1 crosses and six parents were analysed according to Hayman (1954a, b). Diallel analysis was used to compute the variance (V_r) and covariance (W_r) and to construct the W_r/V_r graph. The analysis of variance for the combining ability was done according to method II, model I by Griffing (1956a, b). Statistical analysis of data was conducted by using genetic analysis software (Deck 1988).

Results

Combining ability

Analysis of variance for the combining ability of the genotypes (Table 2) revealed that mean square was highly significant for all characters. All GCA and SCA were highly significant for all of the characters under study in the F_1 generations. Parents' mean squares versus F_1 were highly significant for all traits under this study, except flag leaf length and dry flag leaf weight. The GCA/SCA ratio was very variable, ranged from 0.067 for number of panicle per plant to 0.723 for flag leaf width (Table 2). Low ratio (lower than unity 0.5) of GCA/SCA was found for all characters under study except flag leaf width and flag leaf area.

General combining ability and specific combining ability

The GCA estimated the grain yield of the six parental genotypes (Table 3) and therefore showed that the parents IR69853 and IR65500-127 had the highest and positive GCA indicating that these two parents are good combiners for grain yield. The best general combiners with high

Table 2 Analysis of variance for combining ability effects

Genotype	D.F	Ms				
		Flag leaf width (cm)	Flag leaf length (cm)	Flag leaf area (cm ²)	Length/width ratio (flag leaf)	Chlorophyll content (%)
Genotype	20	0.291**	80.608**	1308.98**	73.416**	58.818**
Parent	5	0.376**	134.411**	705.29**	62.950**	100.726**
F1	14	0.266**	67.106**	1102.97**	79.384**	22.665**
Parents versus F1	1	0.217**	0.613	2211.62**	42.201**	355.426**
Replication	2	0.007	3.200	54.54	0.088	7.934
Error	40	0.004	2.807	90.36	1.517	5.955
GCA	5	0.267**	30.500**	986.002**	19.752**	4.304**
SCA	15	0.040**	25.659**	253.102**	26.045**	8.040**
Error	40	0.001	0.936	30.121	0.506	1.985
<i>Component</i>						
σ^2g		0.028	0.605	91.613	- 0.787	0.782
σ^2s		0.037	24.723	222.980	25.539	16.055
GCA/SCA		0.723	0.149	0.536	0.094	0.173
Genotype	D.F	Ms				
Replication		Dry flag leaf weight (g)	Number of panicles/plant	Number of spikelets/panicle/leaf area	1000-grain weight (g)	Grain yield/plant (g)
Genotype	20	0.326**	54.548**	1.829**	39.206**	4844.88**
Parent	5	0.469**	33.556**	2.584**	38.212**	7236.80**
F1	14	0.006**	56.355**	1.519**	37.821**	3507.71**
Parents versus F1	1	4.098	134.211**	2.392**	63.568**	11,605.74**
Replication	2	0.002	0.492	0.024	2.393	1.59
Error	40	0.006	2.859	0.261	1.050	1.59
GCA	5	0.081**	11.531**	0.878**	8.554**	1891.19**
SCA	15	0.118**	20.400**	0.520**	14.573**	1522.88**
Error	40	0.002	0.953	0.087	0.350	0.53
<i>Component</i>						
σ^2g		- 0.004	- 1.108	0.044	- 0.752	46.04
σ^2s		0.115	19.447	0.433	14.223	1522.35
GCA/SCA		0.085	0.067	0.228	0.072	0.155

Ms mean square, D.F. degree of freedom, σ^2g GCA variance, σ^2s SCA variance, GCA general combining ability, SCA specific combining ability
*, **Significant at 0.05 and 0.01 levels of probability, respectively

positive effects to improve the chlorophyll content, and the number of panicles/plant were the parents Sakha 101 and Giza 178, respectively. The best combiner for flag leaf width, flag leaf length, flag leaf length/width ratio, dry flag leaf and 1000-grain weight was IR65500-127. The SCA estimated for the eight characters presented in Table 4 indicated that the 1 × 2 cross had the best SCA in grain yield. For flag leaf width, the 3 × 5 cross was the best. The 1 × 4 cross had the highest SCA for flag leaf length, length/width ratio, chlorophyll content and number of panicles. The 3 × 6 was the best cross for flag leaf area. 2 × 5 and 2 × 6 were the best crosses for the number of spikelets/panicle/leaf area and 1000-grain weight. The 1 × 4 cross was found to be the best cross for flag leaf length, length

width ratio, chlorophyll content and number of panicle/plant.

Genetic analysis and genetic parameters

Diallel analysis showed that the significance of the additive and non-additive genetic components of variance was just as important in genetic control of all the studied characters for the F1 generation (Table 5). The additive component represents a greater proportion of the non-additive components in all characters under study. The correlation between the b1 component and all the studied characters except flag leaf length was significant. The correlation of b2 and b3 components were significant with all the characters under study.

Table 3 Estimation of general combining ability effects

	Genotype	Traits				
		Flag leaf width (cm)	Flag leaf length (cm)	Flag leaf area (cm ²)	Length/width ratio (Flag leaf)	Chlorophyll content (%)
1	Sakha 101	– 0.108**	– 0.437	6.551**	1.349**	1.570**
2	Giza 178	– 0.256**	– 2.456**	– 18.711**	1.988**	– 3.117**
3	Irat 170	0.068**	– 0.231	– 1.092	– 1.242**	0.657
4	Wab-56-104	– 0.061**	0.001	– 2.730	0.823**	– 0.121
5	IR65500-127	0.274**	3.550**	14.582**	– 1.239**	– 0.507
6	IR69853	0.082**	– 0.426	1.398	– 1.679**	1.519**
S.E. (gi)	0.011	0.312	1.771	0.230	0.455	

	Genotype	Traits				
		Dry flag leaf weight (g)	Number of panicles/plant	Number of spikelets/panicle/leaf area	1000-grain weight (g)	Grain yield/plant (kg)
1	Sakha 101	– 0.087**	1.051**	– 0.092	– 1.506**	– 4.319**
2	Giza 178	– 0.092**	– 0.490	0.622	0.098	– 29.486**
3	Irat 170	0.046**	0.026	– 0.037	– 0.080	7.556**
4	Wab-56-104	– 0.080**	0.088	– 0.013	– 0.746**	7.681**
5	IR65500-127	0.150**	1.339**	– 0.107	1.182**	7.699**
6	IR69853	0.062**	– 2.015**	– 0.374	1.053**	10.931**
S.E. (gi)	0.015	0.315	0.095	0.191	0.235	

S.E. (gi) standard error for GCA effects of parents

*, ** and NS indicate $p < 0.05$, $p < 0.01$ and not significant, respectively

The estimates of the components of genetic variance showed that additive effects (D) were highly significant for all the characters under study except length/width ratio (Table 6). Two standards of dominance—dominance effect (H1) and dominance ratio due to positive and negative influence of genes H2)—were highly significant for the studied traits barring flag leaf area. The “F” value was found to be positive and highly significant for chlorophyll content, dry flag leaf weight, number of panicles/plant, 1000-grain weight and grain yield/plant, showing an excess of the dominant alleles (Table 6). Positive and insignificant “F” value was recorded for flag leaf width, flag leaf length, flag leaf area, length/width ratio and number of spikelets/plant/leaf area. The ratio appearing the degree of dominance $[(H1/D)^{1/2}]$ was higher than one for all the characters showing the presence of over-dominance. In this research, $H2/4H1$ value was above 0.20 for flag leaf width (0.210) and dry flag leaf weight (0.201). The value of this ratio was less than one for all studied characters except chlorophyll content, while the weight of the dry flag leaf was higher than one. The heritability values in the broad sense were higher than the narrow sense values for all the traits in the F1 generation (Table 6). The heritability values in the narrow sense ranged between 0.117 for dry flag leaf weight and 0.666 for flag leaf width. Broad-sense heritability (h^2) values were generally high, they exceeded 0.877 for all traits (Table 6).

Vr/Wr graph

Diallel analysis was used to compute the variance (Vr), covariance (Wr) and to construct the Vr/Vr graph. The Vr/Wr graph (Fig. 1) showed over-dominance for grain yield per plant as the regression line intercepted and the Wr-axis below the point of origin in the F1 generation. The relative dispersion of array points in the graph showed that p5 and p6 took the nearest and the furthest positions from the origin, which determined that these genotypes had the maximum dominant and recessive alleles for grain yield in the F1 generation, respectively. Variation among the cultivars provides options which can be used for possible improvement of hybridization (Abebe et al. 2017).

Discussion

Combining ability

The differences were significant among parents and their crosses regarding GCA and SCA effects. This also suggested the importance of the effects of additive and non-additive genes in the inheritance of the traits under study. The overall genetic control trend of characters can be ascertained for the estimates of the mean square of

Table 4 Estimation of specific combining ability effects

Cross	Traits				
	Flag leaf width (cm)	Flag leaf length (cm)	Flag leaf area (cm ²)	Length/width ratio (flag leaf)	Chlorophyll content (%)
1×2	− 0.151**	2.468**	5.391	4.698**	− 1.082
1×3	− 0.125**	0.373	6.046	1.291**	− 7.429**
1×4	− 0.176**	13.255**	4.461	13.133**	1.499
1×5	− 0.177**	− 2.628**	3.368	− 0.276	0.685
1×6	0.092**	− 0.986	2.458	− 2.168**	− 4.291**
2×3	0.043	− 3.158**	− 15.856**	− 3.643**	− 4.079
2×4	− 0.238**	− 5.070**	− 20.391**	− 0.796	− 1.503
2×5	0.081**	− 4.286**	− 10.543**	− 4.386**	1.089
2×6	0.263**	3.700**	6.251	− 1.445**	− 1.954**
3×4	− 0.062**	0.736	− 17.477**	0.791	− 2.515**
3×5	0.324**	− 1.168	− 19.392**	− 2.616**	− 4.335**
3×6	− 0.127**	− 3.545**	9.522**	− 0.648	0.022
4×5	0.023	− 0.026	− 17.160**	− 0.659	0.950
4×6	0.005	1.910**	5.937	0.875	− 2.283**
5×6	− 0.333**	− 0.640	6.091	3.614	− 0.314
S.E. (Sij)	0.026	0.708	4.017	0.520	1.031

Cross	Traits				
	Dry flag leaf weight (g)	Number of panicles/plant	Number of spikelets/panicle/leaf area	1000-grain weight (g)	Grain yield/plant (kg)
1×2	0.024	− 2.640**	− 0.863**	2.698**	73.012**
1×3	− 0.096**	− 1.163	− 0.094	− 2.715**	32.970**
1×4	0.041	6.108**	0.179	− 4.048**	31.845**
1×5	− 0.178**	− 0.476	− 0.328	0.023	− 26.113**
1×6	− 0.054	− 2.122**	0.252	− 2.181**	54.595**
2×3	− 0.144**	0.715	0.237	− 2.188**	− 24.863**
2×4	− 0.063	− 4.017**	1.080**	0.348	− 24.988**
2×5	− 0.247**	5.399**	0.347	0.420	6.720**
2×6	− 0.108**	− 3.914**	− 0.674**	5.582**	− 4.238**
3×4	− 0.159**	3.606**	0.794**	− 3.474**	− 11.030**
3×5	− 0.312**	4.882**	0.511**	− 3.402**	31.912*
3×6	− 0.271**	2.903**	− 0.4171	− 1.940**	1.720**
4×5	− 0.278**	4.653**	0.875**	− 2.936**	− 23.113**
4×6	− 0.204**	− 1.826**	− 0.051	1.060**	− 4.405**
5×6	− 0.367**	1.737**	− 0.001	3.225**	− 24.113**
S.E. (Sij)	0.033	0.714	0.215	0.433	0.532

S.E. (Sij) standard error for SCA effects of the *i*th and *j*th parents

*, **Significant at 0.05 and 0.01 levels of probability, respectively

GCA and SCA components. In diallel analysis, GCA is a function of additive genetic influences, but it may partly include some dominant effects when the gene frequencies are not equal to one half and/or parents are included in the analysis to estimate variances. However, the SCA is the function of non-additive genetic affects that include dominance and epistatic effects (Hijam et al. 2018).

General combining ability and specific combining ability

The parents had the highest and most positive GCA, indicating that these parents are good combiners for this trait. The effect of SCA is recommended to be used in combination with a high performance per se hybrid, favourable SCA

Table 5 Hayman's Analysis of Variance (ANOVA) for ten traits in 6×6 half-diallel population of rice

Source of variation	D.F	Ms				
		Flag leaf width (cm)	Flag leaf length (cm)	Flag leaf area (cm ²)	Length/width ratio (flag leaf)	Chlorophyll content (%)
a	5	0.267**	30.500**	986.002**	19.752**	24.304**
b	15	0.040**	25.659**	253.102**	26.045**	18.040**
b1	1	0.072**	0.204	737.207**	14.067**	118.475**
b2	5	0.042**	23.425**	396.542**	33.750**	9.465**
b3	9	0.036**	29.728**	119.623**	23.096**	11.645**
error	40	0.001	0.936	30.121	0.506	1.985

Source of variation	D.F	Ms				
		Dry flag leaf weight (g)	Number of panicles/plant	Number of spikelets/panicle/leaf area	1000– grain weight (g)	Grain yield/plant (g)
a	5	0.381**	11.531**	0.878**	14.573**	1891.193**
b	15	0.118**	20.400**	0.520**	8.554**	1522.884**
b1	1	1.366**	44.737**	0.797**	21.189**	3868.580**
b2	5	0.021**	25.480**	0.691**	22.526**	1306.809**
b3	9	0.033**	14.874**	0.395**	9.420**	1382.292**
error	40	0.002	0.953	0.087	0.350	0.529

Ms mean square, D.F. degree of freedom

*, **Significant at 0.05 and 0.01 levels of probability, respectively

estimates, and involving at least one parent with a high GCA (Fasahat et al. 2016).

Genetic analysis and genetic parameter

Significance of the b1 component clarified the dominance deviation in one direction. While, the insignificance of the b1 component for flag leaf length indicated the absence of directional dominance deviation in F1 generation. The significance of the b1 values (asymmetrical gene distribution of dominant and recessive alleles in the F1 generation) illustrates that some parents had more dominant alleles for all studied characters. Therefore, the dominant genetic variance were positive and larger than those of additive genetic variance for traits (El-malky and Al-daej 2018). Whereas, residual dominance due to specific gene complexes was explained by the significance of b3 values in F1 populations, along with the parents. H1 and H2 proposed that additive and non-additive genetic influences were just as important for these characters. Additive and non-additive genetic components of variance were important in the inheritance of the characters (Hasanali-deh et al. 2017). The relative size of the dominance component was higher than that of the additive component, these results are also confirmed by Onyia (2012). Estimates of the “F” value clarified the relative frequency of dominant and recessive alleles in parents,

and this is an indicator of an increase of dominant alleles in the parental lines. Crumpacker and Allard (1962) agreed that if the dominant and recessive alleles of each gene are distributed equally among the parents, the F value will be equal to zero as an indicator of the relative frequency of dominant and recessive alleles. The F value was found to be positive and significantly different from zero. This means that either no alleles display dominance or in this state, among the parents, the dominant and recessive alleles are distributed equally. The ratio $(H1/D) \frac{1}{2}$, showed the presence of over-dominance. From the ratio $H2/4H1$, the symmetrical and asymmetrical distributions in the parents were calculated for the genes. So as to get fast improvement, it is recommended to have parental material where the effect of genes on the characters is symmetrically distributed ($H2/4H1 = 0.25$). The $H2/4H1$ value was above 0.20 for flag leaf width and dry flag leaf weight clarifying the symmetrical distribution of the genes. The number of the effective factors controlling the particular traits were shown by the $h2/H2$ ratio. The value of this ratio was less than one, illustrating that one gene was controlling these characters, while this ratio was greater than one, it proposed that a dominant gene was controlling the character. The heritability values in the broad sense were higher than the narrow sense values, which identified higher variability than the environmental impacts of these trait values.

Table 6 Components of variance and stability estimates for different traits in rice

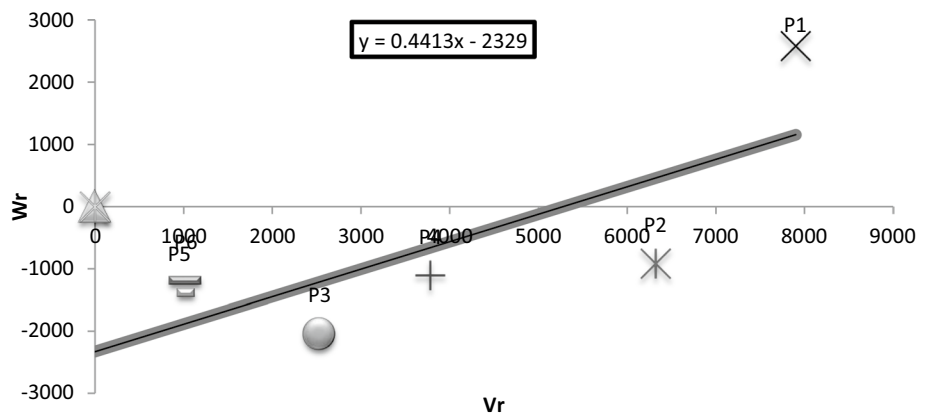
Variance components	Traits				
	Flag leaf width (cm)	Flag leaf length (cm)	Flag leaf area (cm ²)	Length/width ratio (flag leaf)	Chlorophyll content (%)
D	0.124 ± 0.012**	43.86 ± 18.31*	538.87 ± 163.8**	20.500 ± 16.839	31.559 ± 6.368**
F	0.007 ± 0.030	67.12 ± 44.73	384.01 ± 200.25	46.771 ± 41.137	40.080 ± 5.556**
H1	0.164 ± 0.031**	119.42 ± 46.4*	1066.91 ± 415.91*	123.06 ± 42.74**	63.089 ± 16.165**
H2	0.138 ± 0.028**	81.41 ± 41.52*	656.15 ± 71.54	79.915 ± 38.187*	45.495 ± 4.441**
h2	0.046 ± 0.019*	- 0.39 ± 27.94	461.40 ± 50.07	25.702 ± 8.849	75.669 ± 9.719**
(H1/D) ^{1/2}	1.148	1.650	1.407	2.450	1.414
H2/4H1	0.210	0.170	0.154	0.162	0.180
h2/H2	0.33	0.09	0.70	0.11	1.66
KD/KR	1.054	2.730	1.678	2.742	2.631
h ² n	0.666	0.257	0.594	0.292	0.253
h ² b	0.988	0.967	0.938	0.983	0.888

Variance components	Traits				
	Dry flag leaf weight (g)	Number of spikelets/ panicle/leaf area	Number of panicles/plant	1000-grain weight (g)	Grain yield/plant (g)
D	0.154 ± 0.02**	10.27 ± 4.55**	0.778 ± 0.25*	12.366 ± 2.505**	2411.73 ± 611.01**
F	0.204 ± 0.055**	29.820 ± 11.12	1.158 ± 0.629**	33.153 ± 6.120**	3500.28 ± 1492.70**
H1	0.350 ± 0.057**	90.065 ± 1.556**	2.242 ± 0.653**	69.861 ± 6.359**	6690.56 ± 1551.11**
H2	0.281 ± 0.051**	58.922 ± 0.324*	1.356 ± 0.584**	40.285 ± 5.681**	4630.34 ± 1385.64**
h2	0.884 ± 0.034**	28.488 ± 6.94	0.471 ± 0.39**	13.528 ± 3.8**	2507.11 ± 932.63**
(H1/D) ^{1/2}	1.506	2.961	1.697	2.377	1.666
H2/4H1	0.201	0.164	0.151	0.144	0.173
h2/H2	3.150	0.480	0.350	0.34	0.54
KD/KR	2.570	2.924	2.562	3.587	2.544
h ² n	0.117	0.270	0.374	0.296	0.295
h ² b	0.976	0.957	0.877	0.974	0.997

D additive variance; H1, H2 and h2 dominance variance; F product of additive and dominance alleles; E environmental variance; (H1/D)^{1/2} degree of dominance; H2/4H1 balance of positive and negative alleles; h2/H2 number of effective factors; KD/KR the proportion of dominant to recessive genes; h²b broad-sense heritability; h²n narrow sense heritability

*, **Significant at 0.05 and 0.01 levels of probability, respectively

Fig. 1 Vr/Wr graph for grain yield/plant



The values of heritability (h²n) were lower, especially mostly for traits with the lowest GCA/SCA proportions. Broad-sense heritability (h2) values were generally

high indicating that most of the variations observed were genetically determined and that selection among the varieties or hybrids will be efficient.

Conclusions

Our study provides general information relevant to some flag leaf and yield characters breeding for the development of F1 rice hybrids. The highly significant differences observed for GCA and SCA for all traits indicates that there is a large genetic diversity in the group of parents and crosses that can be used for breeding. Under this study, IR65500-127, Giza 178, and Sakha 101 were identified as good parents; therefore, these parents are suggested for further recombinant breeding programmes. The cross 3 × 5 was found to be superior for flag leaf width and grain yield, while the cross 1 × 4 was found to be superior for flag leaf length, flag leaf length/width ratio, chlorophyll content and number of panicles/plant. The graphical analysis dependent on the position of the regression line showed that over-dominance played an important role in the inheritance of gene action for grain yield/plant. Broad-sense heritability values were generally high indicating that most of the variations observed were genetically determined and that the selection among the varieties or hybrids would be efficient. On the base of the differences we found in GCA/SCA ratios and heritability, we consider crossing a fast and appropriate strategy to develop improved rice cultivars.

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References

- Abebe T, Alamerew S, Tulu L (2017) Genetic variability, heritability and genetic advance for yield and its related traits in rainfed lowland rice (*Oryza sativa* L.) genotypes at Fogera and Pawe, Ethiopia. *Adv Crop Sci Technol* 5:272. <https://doi.org/10.4172/2329-8863.1000272>
- Acquaah G (2007) Principles of plant genetics and breeding. *Crop Sci* 47(4):1763
- Bagheri N (2010) Heterosis and combining ability analysis for yield and related-yield traits in hybrid rice. *Int J Biol* 2(2):222–231
- Christie BR, Shattuck VI (2010) The diallel cross: Design, analysis, and use for plant breeders. *Plant Breed Rev* 9:9–36. <https://doi.org/10.1002/9780470650363>
- Crumpacker DW, Allard RW (1962) A diallel analysis of heading date in wheat. *Hilgardia* 32:275–278
- Deck JA (1988) Genetic analysis program. Ontario Agricultural College, Guelph
- El-malky MM, Al-daej M (2018) Studies of genetic parameters and cluster analysis of some quantitative characters through diallel analysis of rice (*Oryza sativa* L.). *Vegetos* 31:1
- Fasahat P, Rajabi A, Rad JM, Derera J (2016) Principles and utilization of combining ability in plant breeding. *Biom Biostat Int J*. 4(1):1–22. <https://doi.org/10.15406/bbij.2016.04.00085>
- Griffing B (1956a) A generalized treatment of the use of diallel crosses in quantitative inheritance. *Heredity* 10:31–50
- Griffing B (1956b) Concept of general and specific combining ability in relation to diallel crossing systems. *Aust J Biol Sci* 9:463–493
- Hasanalideh AH, Farshadfar E, Allahgholipour M (2017) Genetic parameters and combining ability of some important traits in rice (*Oryza sativa* L.). *Genetika* 49(3):1001–1014. <https://doi.org/10.2298/GENSR1703001H>
- Hayman BI (1954a) The analysis of variance of diallel tables. *Biometries* 10:235–244
- Hayman BI (1954b) The theory and analysis of diallel crosses. *Genetics* 39:789–809
- Hijam C, Singh NB, Laishram JM (2018) Diallel analysis of yield and its important components in aromatic rice (*Oryza sativa* L.). *Indian J Agric Res* 53(1):67–72 (ISSN:0976-058X)
- Khatun MT, Hanafi MM, Yusop MR, Wong MY, Salleh FM, Ferdous J (2015) Genetic variation, heritability, and diversity analysis of upland rice (*Oryza sativa* L.) genotypes based on quantitative traits. *BioMed Res Int* 6:1–7
- Onyia VN (2012) Combining ability analysis for yield and yield components in eight breeding lines of rice (*Oryza sativa* L.). *J Trop Agric Foods Environ Ext* 10(2):7–15
- Pauk J, Jancsó M, Simon-Kiss I (2009) Rice doubled haploids and breeding. In: Touraev A, Forster BP, Jain SM (eds) *Advances in haploid production in higher plants*. Springer, Dordrecht
- Rahimi M, Rabiei B, Samizadeh H, Ghasemi A (2010) Combining ability and heterosis in rice (*Oryza sativa* L.) cultivars. *J Agric Sci Technol* 12:223–231
- Rahman Md, Haque M, Sikdar B, Islam Md, Matin M (2014) Correlation analysis of flag leaf with yield in several rice cultivars. *J Life Earth Sci* 8:49–548. <https://doi.org/10.3329/jles.v8i0.20139>
- Shang F, Chao X, Meng K, Meng X, Li Q, Chen L, Wang J (2020) Fine mapping of a grain shape gene from a rice landrace longliheinuodwarf (*Oryza sativa* L. ssp. japonica). *Agronomy* 10:380. <https://doi.org/10.3390/agronomy10030380>
- Singh AK, Chaudhary BD (1985) *Biometrical Methods in quantitative genetic analysis*. Kalyani Publisher, New Dehli
- Snedecor GW, Corchran WG (1989) *Statistical methods*, 8th edn. Iowa State University Press, Iowa
- Tian Y, Zhang H, Xu P, Chen X, Liao Y, Han B (2015) Genetic mapping of a QTL controlling leaf width and grain number in rice. *Euphytica* 202(1):1–11
- Tsukaya H (2006) Mechanism of leaf-shape determination. *Annu Rev Plant Biol* 57:477–496. <https://doi.org/10.1146/annurev.arplant.57.032905.105320> (PMID: 16669771)
- Wang Y, Pang Y, Chenc K, Zhaia L, Shenc C, Wang S, Xus J (2020) Genetic bases of source-, sink-, and yield-related traits revealed by genome-wide association study in Xian rice. *Crop J* 81:19–131
- Yoshida S, Forno DA, Cock JH, Gomez KA (1976) *Laboratory manual for physiological studies of rice*. International Rice Research Institute, Los Banos, Laguna, p 83