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Full Length Article

Combining Ability and Heritability Analysis Provide Insights into Variability for Multiple Agronomic Traits in Two-Line Hybrid Black Rice

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Abstract

To analyze the combining ability and heritability of the main agronomic traits in black rice parents, and thus provide a theoretical basis for parent seed selection of two-line hybrid black rice and screening of superiority combinations. The combining ability and heritability of eight main agronomic traits were analyzed by 6×5 incomplete diallel cross (NCII) model through 6 sterile lines and 5 restorer lines. The results showed a significant difference in combining ability variance of the studied agronomic traits. The seed setting rate is mainly controlled by special combining ability of the combination. The effective panicle number is mainly controlled by general combining ability of the parents. The other agronomic traits are controlled by special combining ability of the combination together with general combining ability of the parents. From big to small, the narrow heritability is in the order of plant height, thousand seed weight, panicle length, spikelets per panicle, filled spikelets per panicle, yield per plant, effective panicle and seed setting rate. Multiple agronomic traits in two-line sterile line D18S, D40S and restorer line R401 of black rice have high effect value in terms of general combining ability and special combining ability, and the application prospect is bright.

Key words: Diallel cross; Two line hybrid; Yield

Introduction

The black rice is rich in nutrients particularly anthocyanins, proteins, amino acids and trace elements. It has also high nutritional and health care value (Kim *et al.*, 2013; Kushwaha, 2016; Ghasemzadeh *et al.*, 2018), because of its anti-oxidation, anti-aging, hypolipidemic, anti-inflammatory and anti-tumor production functions (Phetpornpaisan *et al.*, 2014; Biswas *et al.*, 2018; Ma *et al.*, 2018). However, black rice breeding level is still insufficient due to problems such as high plant height, long growth period and low yield, its further promotion and application are also greatly limited (Luo, 2014; Li *et al.*, 2015; Wooduck *et al.*, 2015). An effective way to solve these problems is to exploit heterosis in black rice (Haghighi *et al.*, 2017). Sterile lines and restorer lines constitute important germplasm resources for black rice breeding. Combining ability determination is an important link in seed selection of rice or two-line hybrid black rice (Samrath and Deepak, 2015; Santha *et al.*, 2016; Zhu *et al.*, 2018). Scientific prediction of combining ability of two-line hybrid black rice parent can help to improve breeding efficiency, which means great significance for rational combination of two-line hybrid black rice, and for black rice production as well as satisfaction of diversified demand for market diversification and specificity.

Initial success has been achieved in seed selection of black rice in conventional varieties, including 'Nunkeunheugchal', 'Wanxianzibao', 'Xiangheimi' and 'Wugong No.1' (Luo, 2014; Li *et al.*, 2015; Wooduck *et al.*, 2015). In terms of heterosis exploitation of black rice, hybrid rice breeding lacks innovative ability, conventional varieties dominate its production and application, and a few three-line sterile lines of black rich have been bred, including 'Xuehei A', 'Xiangxuejing A' and '186A' (Sun *et al.*, 2013). Seed selection of two-line hybrid black rice also lags behind. And there are few studies on genetic characteristics of agronomic traits in hybrid black rice. Studies have shown that non-additive effect of genes plays a dominant role in duration from seeding to heading and effective panicle number per plant of three-line hybrid black rice, while additive effect of genes plays a dominant role in plant height, panicle length, spikelets per panicle and filled spikelets per panicle. Moreover, the additive and non-additive effects of genes play a relatively important role in trait expression of seed setting rate, thousand seed weight and

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yield per plant (Liu, 2011).

The sterile and restorer lines selected in this study are newly selected black rice parents. The leaves are well-formed, the brown rice is black, and quality is excellent, which makes it important germplasm resources for combination of two-line hybrid black rice. At present, there is no report on genetic characteristics of agronomic traits in two-line hybrid black rice.

With 6 sterile lines, 5 restorer lines and 30 prepared hybrid combinations as material and genetic regularity of main agronomic traits in two-line hybrid black rice will be studied *via* incomplete diallel cross experiment to provide technical support for parent apolegamy, combination measurement and evaluation of two-line hybrid black rice.

Materials and Methods

Experimental Material

In Zhaoan, Fujian, China in 2016, with newly selected 6 two-line sterile lines of black rice including D18S, D38S, D40S, D43S, 272S and 48S as female parents, as well as 5 two-line restorer lines of black rice including R48, R92, R149, R156 and R401 as male parents, 30 two-line hybrid black rice combinations were prepared according to incomplete diallel cross (NCII).

Method

On November 20th, 2016, 30 black rice hybrid combinations plus parents were planted in Sanya, Hainan, China. On December 20th, the test combinations and parents were transplanted. The experiment was arranged in random blocks, and 3 repetitions. For each plot, rice seedlings were transplanted according to 8 plants × 8 rows = 64 plants, and the plant spacing was 20 cm × 20 cm. Single rice seedling were transplanted. Flood irrigation, fertilizer (200 kg·ha^{-1} N, 60 kg·ha^{-1} P_2O_5, 60 kg·ha^{-1} K_2O, and 30 kg·ha^{-1} Zn) and chemical weed control was applied. The initial heading stage, duration from seeding to heading, mature stage of the parent and the combination were recorded. For each plot, the five plants in the middle were selected for plant test, and eight agronomic traits of hybrid black rice combination and parent, including plant height, effective panicle, panicle length, total particle number per single panicle, number of full grains per single panicle, seed setting rate, thousand seed weight and yield per plant, were measured and counted.

Statistical Analysis

The software Microsoft Excel 2007 was used to preliminarily arrange and calculate the data. Combining ability was analyzed based on NCII hybrid model, seed setting rate was converted through arcsine square root in variance and combining ability analysis. The values of general combining ability, special combining ability and other genetic parameters were calculated by DPS software (Tang, 2013).

Results

Variance Analysis and Combining Ability of Agronomic Traits

There was significant or extremely significant level in mean square value difference of the test combinations, indicating genetic difference. The combining ability analysis showed that except seed setting rate and thousand seed weight, general combining ability variance of female parent with respect to the other six agronomic traits achieved significant or extremely significant level (Table 1). It suggests that sterile line plays an important role in the six traits of the prepared combinations, which exerts little effect on performance of seed setting rate and thousand seed weight. Except male parent restorer line which exerts little effect on effective panicle and seed setting rate, it significantly or extremely significantly influences general combining ability of the other six agronomic traits, indicating the role of male parents into six agronomic trait combinations. The six traits of the test combinations, including plant height, panicle length, spikelets per panicle, filled spikelets per panicle, thousand seed weight and yield per plant are co-determined by general combining ability of the parents and special combining ability of the combination. The effective hybrid panicle is mainly determined by general combining ability of sterile line. The hybrid seed setting rate is mainly determined by special combining ability of the combination, while thousand seed weight of the hybrid is mainly determined by general combining ability of male parent restorer and special combining ability of the combination.

Effect Analysis on General Combining Ability of Parents

There exist obvious differences between the traits of the test parents in terms of effect value of general combining ability (GCA), also GCA of each parent differs greatly for the same trait, suggesting that parents have different additive effects for different traits, and the additive effect of parent on the same trait also differs (Table 2).

GCA of black rice sterile line D18S was high in traits such as plant height, panicle length, spikelets per panicle, filled spikelets per panicle and yield per plant. GCA of D40S was also high in such traits as plant height, effective panicle, panicle length, spikelets per panicle, filled spikelets per panicle, thousand seed weight, and yield per plant. In terms of black rice restorer line, R401 showed great GCA in the studied agronomic traits. And R149 showed great GCA for plant height, effective panicle, panicle length, thousand seed

Table 1: Variance analysis and combining ability of 30 hybrids on agronomic traits

Variation source	PH	EP	PL	SPP	FSPP	SSR	TSW	YPP
Combinations	186.091**	6.964*	9.546**	2950.919**	2639.096**	0.0036**	9.401**	285.724**
S	673.906**	6.350**	35.558**	5274.212**	4225.018**	0.0081	56.300	875.285*
R	389.118**	17.884	18.668**	7700.203*	6632.653*	0.0009	3.561**	476.353**
S×R	23.532**	4.357	2.063**	1298.939**	1323.523**	0.0034**	1.482**	120.154*
Error	2.457	3.917	0.497	298.988	283.145	0.0012	0.358	68.185

PH: plant height; EP: effective panicle; PL: panicle length; SPP: spikelets per panicle; FSPP: filled spikelets per panicle; SSR: seed setting rate; TSW: thousand seed weight; YPP: yield per plant; S: female parent ; R: male parent; *: significant difference at $P < 0.05$; **: significant difference at $P < 0.01$

Table 2: The effect values of general combining ability of parents on agronomic traits

Parent	PH	EP	PL	SPP	FSPP	SSR	TSW	YPP
D18S	5.816	-3.612	2.469	15.276	15.039	-0.225	-0.589	14.254
D38S	-3.351	6.654	-0.259	-14.655	-14.049	0.826	2.444	-5.478
D40S	9.569	0.380	3.831	10.106	9.746	-0.225	1.106	11.957
D43S	-0.420	10.646	4.409	-13.031	-13.403	-0.726	0.570	-1.307
272S	-9.052	-16.160	-7.484	11.092	11.126	-0.225	-0.749	-9.572
48S	-2.563	2.091	-2.966	-8.789	-8.462	0.576	-2.781	-9.853
R48	-6.840	-4.943	-7.623	-11.144	-10.734	0.593	-4.467	-19.778
R92	-0.776	-3.992	2.924	12.858	11.321	-2.120	-7.604	-1.147
R149	4.215	0.761	4.184	-0.488	-1.363	-1.202	8.180	8.924
R156	-1.109	7.890	-4.699	-8.668	-7.796	1.135	-1.064	-2.656
R401	4.510	0.285	5.214	7.442	8.572	1.595	4.955	14.657

PH: plant height; EP: effective panicle; PL: panicle length; SPP: spikelets per panicle; FSPP: filled spikelets per panicle; SSR: seed setting rate; TSW: thousand seed weight; YPP: yield per plant

weight and yield per plant. Therefore, D18S and D40S are the two female parents with fine general combining ability, while R401 and R149 are the male parents with good general combining ability in agronomic traits.

Effect Analysis of Special Combining Ability

There was also significant difference in special combining ability (SCA) for different combinations of the same trait (Table 3). Among different combinations, D18S/R149 showed higher or the highest SCA effect for agronomic traits; D18S/ R401 also showed higher or the highest SCA effect for plant height, effective panicle, panicle length, spikelets per panicle, filled spikelets per panicle, seed setting rate and yield per plant; D38S/R92 with high SCA effect for effective panicle, seed setting rate, thousand seed weight, and yield per plant; D38S/R156 with higher or the highest SCA effect for plant height, effective panicle, panicle length, spikelets per panicle, filled spikelets per panicle, seed setting rate and yield per plant; D40S/R48 with high SCA effect for plant height, panicle length, spikelets per panicle, filled spikelets per panicle and seed setting rate and D43S/R156 with high SCA effect for plant height, effective panicle, panicle length, spikelets per panicle, filled spikelets per panicle and yield per plant. Therefore, these six combinations have fine SCA in multiple agronomic traits.

Agronomic Trait Population Variance and Heritability Estimation

The general combining ability and special combining ability play different roles in the inheritance of the agronomic traits (Table 4). In the inheritance of these agronomic traits, general combining ability had a large proportion (Vg>50%), indicating that among these traits, genetic additive effect of parents plays a dominant role in the formation of the first generation of hybrid trait. Specific combining ability accounts for a large proportion (Vs>50%) in the inheritance of seed setting rate, suggesting that in seed setting rate, non-additive effect of parental genes plays a leading role in the formation of the first generation of hybrid trait. The interaction of the two parents plays an un-negligible role in terms of seed setting rate.

The general combining ability of sterile line and restorer line plays different roles in the inheritance of different traits (Table 4). In traits such as plant height, effective panicle, spikelets per panicle, filled spikelets per panicle and GCA genotypical variance of sterile line takes up larger proportion as compared to male parent ($Vg_1>Vg_2$), indicating that genotypical variance of sterile lines contribute more to variance of general combining ability when it comes to these traits. For traits including panicle length, seed setting rate, thousand seed weight and yield per plant, GCA genotypical variance takes up larger proportion as compared to female parent ($Vg_1<Vg_2$), suggesting that restorer line plays greater role in these traits.

The narrow heritability of the agronomic traits is in the order of plant height > thousand seed weight > panicle length > spikelets per panicle > filled spikelets per panicle > yield per plant > effective panicle > seed setting rate (Table 5). Plant height, thousand seed weight and panicle length

Table 3: The effects value of special combining ability of agronomic traits

Combination	PH	EP	PL	SPP	FSPP	SSR	TSW	YPP
D18S/R48	-3.802	-0.190	-4.031	3.467	3.912	0.309	-1.814	-1.822
D18S/R92	0.816	-9.696	-0.538	-14.034	-13.862	0.267	0.905	-21.644
D18S/R149	1.467	16.920	3.695	7.832	4.177	-4.157	0.251	29.733
D18S/R156	-0.753	-13.023	-0.600	1.171	2.101	0.768	0.848	-14.537
D18S/R401	2.273	5.989	1.473	1.564	3.673	2.813	-0.190	8.271
D38S/R48	-2.647	-13.308	-0.371	5.439	5.041	-0.242	1.045	-4.569
D38S/R92	-1.601	14.259	-1.905	-9.860	-8.228	2.221	0.861	6.607
D38S/R149	3.790	-10.456	1.835	1.826	2.066	0.050	0.100	-10.126
D38S/R156	0.836	5.228	2.444	3.293	2.179	-1.787	-2.198	6.391
D38S/R401	-0.377	4.278	-2.003	-0.700	-1.058	-0.242	0.196	1.696
D40S/R48	0.124	-1.331	1.909	0.892	2.262	2.062	-0.040	-1.213
D40S/R92	-0.733	11.977	-5.023	-15.187	-20.437	-5.994	1.781	2.722
D40S/R149	-0.216	-9.886	0.580	3.311	5.986	3.356	1.065	-7.059
D40S/R156	-1.034	2.947	-1.673	-0.619	0.447	1.269	0.087	2.934
D40S/R401	1.859	-3.707	4.208	11.604	11.743	-0.693	-2.894	2.615
D43S/R48	1.900	-0.190	-2.341	-3.775	-3.865	-0.192	0.201	-4.981
D43S/R92	-0.827	-3.992	1.303	-5.914	-6.744	-1.736	1.628	-5.157
D43S/R149	-0.844	-3.042	-1.765	0.959	3.137	3.105	-0.994	-5.695
D43S/R156	1.443	6.939	3.310	1.538	1.697	0.518	-0.680	5.809
D43S/R401	-1.673	0.285	-0.507	7.191	5.775	-1.695	-0.155	10.024
272S/R48	3.722	-1.901	1.539	1.330	1.397	0.309	0.093	3.800
272S/R92	5.202	-5.703	7.812	39.007	41.434	3.022	-5.959	14.800
272S/R149	-4.095	-1.901	-3.365	-13.901	-14.743	-1.152	3.904	-9.791
272S/R156	-3.845	5.228	-4.043	-9.649	-10.673	-1.486	-1.982	-1.812
272S/R401	-0.985	4.278	-1.943	-16.787	-17.415	-0.693	3.943	-6.998
48S/R48	0.704	16.920	3.295	-7.353	-8.747	-2.246	0.514	8.785
48S/R92	-2.856	-6.844	-1.650	5.987	7.837	2.221	0.784	2.671
48S/R149	-0.102	8.365	-0.979	-0.026	-0.622	-1.202	-4.323	2.938
48S/R156	3.353	-7.319	0.562	4.266	4.251	0.718	3.925	1.214
48S/R401	-1.098	-11.122	-1.228	-2.874	-2.718	0.509	-0.901	-15.608
Variation	-4.095~5.202	-13.308~16.920	-5.023~7.812	-16.787~39.007	-20.437~41.434	-5.994~3.356	-5.959~3.943	-21.644~29.733

PH: plant height; EP: effective panicle; PL: panicle length; SPP: spikelets per panicle; FSPP: filled spikelets per panicle; SSR: seed setting rate; TSW: thousand seed weight; YPP: yield per plant

Table 4: Genotypical variance of agronomic traits

Trait	Genotypical variance			Vg/%	Vs/%	Vg_1%	Vg_2%
	δ_1	δ_2	δ_{12}				
PH	43.358	20.310	7.025	90.06	9.94	61.33	28.73
EP	0.902	0.111	0.147	87.33	12.67	77.76	9.55
PL	1.107	1.861	0.522	85.04	14.96	31.72	53.32
SPP	426.751	220.849	333.317	66.02	33.98	43.51	22.51
FSPP	353.942	161.194	346.793	59.77	40.23	41.06	18.70
SSR	0.0001	0.0003	0.0007	36.36	63.64	9.09	27.27
TSW	0.139	3.046	0.375	89.47	10.53	3.90	85.56
YPP	23.747	41.951	17.323	79.13	20.87	28.60	50.53

PH: plant height; EP: effective panicle; PL: panicle length; SPP: spikelets per panicle; FSPP: filled spikelets per panicle; SSR: seed setting rate; TSW: thousand seed weight; YPP: yield per plant; δ_1: GCA genotypical variance of female parent; δ_2: GCA genotypical variance of male parent; δ_{12}: genotypical variance of parental interaction; Vg: proportion of GCA genotypical variance in total variance; Vs: proportion of SCA genotypical variance in total variance; Vg_1: proportion of GCA genotypical variance of female patent in total variance; Vg_2: proportion of GCA genotypical variance of male patent in total variance

Table 5: The heritability of agronomic traits

Parent	PH	EP	PL	SPP	FSPP	SSR	TSW	YPP
broad-sense heritability	96.64	22.84	87.55	76.64	75.27	44.71	90.86	54.91
narrow-sense heritability	87.04	19.95	74.45	50.60	44.99	11.63	81.30	43.45

PH: plant height; EP: effective panicle; PL: panicle length; SPP: spikelets per panicle; FSPP: filled spikelets per panicle; SSR: seed setting rate; TSW: thousand seed weight; YPP: yield per plant

have high heritability, indicating that these traits can be selected in the early generation during breeding to improve breeding efficiency, while seed setting rate and effective panicle have low heritability, which are unsuitable for selection in lower generation.

Discussion

The present study showed that genetic regularity of the studied agronomic traits in black rice is jointly controlled by additive and non-additive genes. The GCA accounts for a significant proportion in the inheritance of seven traits including plant height, effective panicle, panicle length, spikelets per panicle, filled spikelets per panicle, thousand seed weight and yield per plant. In these traits, genetic additive effect of parents plays a dominate role in the formation of the first generation of hybrid trait. SCA accounts for a large proportion in the inheritance of seed setting rate, suggesting that in terms of seed setting rate, non-additive effect of parental gene plays a dominant role in the formation of the first generation of hybrid trait (Zong *et al*., 2006). Liu (2011) found in hybrid black rice that additive gene effect of parents accounts for a significant proportion in the inheritance of plant height, panicle length, spikelets per panicle and filled spikelets per panicle, meanwhile, both additive and non-additive gene effects play an important role in the traits including seed setting rate, thousand seed weight and yield per plant. Haghighi *et al.* (2017) found in white rice that GCA and SCA were significant for effective panicle, filled spikelets per panicle, 1000-seed weight and yield per plant indicating the involvement of additive and non-additive effects. Liu *et al.* (2016) found in hybrid white rice that additive effect of parental gene plays a dominant role in the inheritance of panicle length, spikelets per panicle, filled spikelets per panicle, seed setting rate and thousand seed weight; and non-additive effect of parental gene plays a dominant role in the inheritance of plant height, effective panicle and yield per plant. Qi and Sheng (2000) found in hybrid white rice that additive effect of parental gene plays a dominant role in the inheritance of plant height, panicle length, spikelets per panicle, filled spikelets per panicle and thousand seed weight; and non-additive effect of parental gene plays a dominant role in the inheritance of effective panicle, seed setting rate and yield per plant. As shown above, there are different results between different studies on inheritance of agronomic traits in different rice.

It can be seen from the present study that yield per plant of variety 272S/R92 has high special combining ability, while varieties 272S and R92 have low general combining ability. Therefore, it is possible to prepare hybrid black rice combination with high special combining ability using black rice material with low combining ability is consistent with previous studies (Qi and Sheng, 2000; Ni *et al*., 2009; Liu *et al*., 2016; Haghighi *et al*., 2017). Fine parent can gather more favorable genes (Dorosti and Monajjem, 2014). If two fine parents are matched, new rice varieties of hybrid black rice with great advantages can be prepared by taking advantage of their additive and non-additive effects. In this study, D18S has the highest general combining ability among yield per plant of sterile line, while all hybrid rice combinations matched with restorer lines R149 and R401 with high general combining ability and very high special combining ability. Therefore, to improve the breeding efficiency of hybrid black rice, parents with high general combining ability, and carry out broad test crosses should be bred, in order to obtain hybrid black rice combination with high yield.

The effect of general combining ability of sterile line and restorer line on the first generation of hybrid, general combining ability of sterile line plays a dominant role in the four traits including plant height, effective panicle, total particle number of panicle and filled spikelets per panicle, while general combining ability of restorer line plays a dominant role in panicle length, seed setting rate, thousand seed weight and yield per plant (Zong *et al*., 2006; Liu *et al.*, 2016). It suggests that in seed selection of high yield hybrid black rice, there should be different emphasis on improvement and selection of sterile lines and restorer lines. In seed selection of sterile lines, emphasis should be given to the selection of tillering power and grain number, and plant height should be appropriately lowered; in seed selection of restorer lines, emphasis should be given to large panicle, large grain and high seed setting rate so that heterosis of hybrid black rice can be improved, which is consistent with previous studies (Liu *et al.*, 2016).

According to GCA and SCA, parents can be divided into four types: the first type features high GCA and great SCA, which constitutes the most ideal parent; the second type features high GCA and low SCA, which constitutes fine parent; the third type features low GCA and great SCA, which constitutes parent with certain use value; the fourth type features low GCA and SCA, which constitutes parent basically with no use value (Zong *et al*., 2006; Lei *et al.*, 2017). By synthesizing combining ability of agronomic traits in black rice sterile and restorer lines, it can be found that two-line black rice sterile lines D18S, D40S and R401generally perform well in agronomic traits in terms of general and special combining ability, D18S, D40S are ideal two-line black rice sterile lines, and R401 is ideal black rice restorer line. D18S, D40S and R401 enjoy great application prospects in production. Through extensive test crosses and matching, it is possible to select high-yield superiority combinations with good special combining ability in agronomic traits.

Conclusion

The combining ability analysis results in this study showed that sterile line D18S has great GCA in such traits as plant height, panicle length, total particle number of panicle, filled spikelets per panicle and yield per plant; sterile line D40S also has great GCA in such agronomic traits as plant height, effective panicle, panicle length, spikelets per panicle, filled spikelets per panicle, thousand seed weight and yield per plant; black rice restorer line R401 has great GCA in all studied traits. Therefore, several agronomic traits of two-line black rice sterile lines D18S, D40S and black rice restorer line R401 have high effect value in general and special combining ability, enjoying bright application prospects.

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