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Combining Ability Effects for Various Agro-Morphological Traits in Rice under Temperate Conditions

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Authors' contributions

This work was carried out in collaboration among all authors. Authors AM, GAP, NRS, ABS and SAW designed the study, performed the statistical analysis, wrote the protocol and wrote the first draft of the manuscript. Authors NRS, ABS and SAW managed the analyses of the study. Author SAW managed the literature searches. All authors read and approved the final manuscript.

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ABSTRACT

Rice is one of the most consumed food crops in the world and therefore possesses huge socio-economic relevance. Combining ability estimates provide the basis for selection of suitable parents in breeding programmes for rice improvement. The experiment was conducted to evaluate the combining ability effects for various agro-morphological traits in some genotypes of rice. Thirty-four male parents were crossed with the four CMS lines in line × tester matting design and 136 cross combinations were obtained. For most of the traits, SKUA-7A showed desirable GCA effect among the female parental lines; while RL-1, RL-2, RL-11, SKUA-497, SKUA-494, SKUA-496 and SKUA-420 showed desirable GCA effect amongst the male parents. Cross combinations SKUA-7A × RL-3 and SKUA-11A × RL-5 revealed desirable heterosis for most of the traits *viz.,* grain yield, number of effective tillers plant^{-1}, panicle length and number of spikelet panicle^{-1}. These cross combinations also possessed desirable values of SCA effect. In general, the cross combinations showing desirable specific combining ability effects also reveal better per se performance for the respective traits.

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1. INTRODUCTION

Among all the cereal crops, rice is the most important food crop and it has been estimated that more than half of the world's population subsists wholly or partially on rice [1]. The rising demand, saturation of cultivable fields and low gross domestic production of rice are likely to cause a supply shortage of the crop in near future. Global rice production will have to increase by 70 percent by 2050 to meet the food requirements of ever-growing population [2]. Rice being the main staple food for major portion of the Indian population, improving its production has become crucially important [3]. The increase in productivity of rice is the only option left with plant breeders under the circumstances of shrinkage of land area under the crop and the availability of less water, less labour and increase in cost of cultivation. Exploitation of heterosis in the form of hybrid rice technology has been contemplated as a potential strategy for yield enhancement in rice, which has successfully been demonstrated by China after the commercial release of hybrids.

Among the plethora of genetic approaches for improving rice productivity, hybrid rice has fared well and it has been anticipated that hybrid rice technology will play a key role in ensuring food security worldwide in the future decades. The hybrid rice technology leads to the increase in yield potential of rice varieties by 15 to 20 percent over the pure line commercial cultivars. In India, the average productivity of rice is about 4 t ha^{-1} and hybrid rice varieties can produce a marked improvement of up to 1-1.5 t ha^{-1} [4,5]. Among the various approaches, three-line system has become a practical option for hybrid production in rice. In this system, cytoplasmic male sterility (CMS) has an essential role to play in hybrid development.

Combining ability effects, aids in the selection of desirable parents and crosses for the exploitation of heterosis or hybrid vigour. Variance due to general and specific combining ability effects represents the relative measure of additive and non-additive gene actions, respectively. Breeders exploit these variance components to evaluate the gene action and to assess the genetic potentiality of parents in different cross combinations [6]. A number of mating designs have been proposed to assess the relative magnitude of the genetic component of variance. Among these, line × tester design is being commonly used because it is more manageable with large number of genotypes [7]. This method gives an overall genetic picture of the material under investigation in a single generation. The present study was conducted to assess the general combining ability and specific combining ability for various agro-morphological traits in rice.

2. MATERIALS AND METHODS

The present study was conducted at Mountain Research Centre for Field Crops [MRCFC (Khudwani), SKUAST of Kashmir, Jammu & Kashmir, 33°70' N latitude and 75°10' E longitude; 1680 amsl], during *Kharif* seasons of 2017 and 2018. Twelve plant characters *viz.,* days to 50% flowering, plant height (cm), Flag leaf area (cm^2), effective tillers $plant^{-1}$, panicle length (cm), spikelets $panicle^{-1}$, test weight (g), grain yield (t ha^{-1}), biological yield (t ha^{-1}), harvest index (%), kernel length and kernel width were studied in the experiment.

Statistical analysis of the data was carried out using Windostat Software version 9.1. Combining ability analysis was carried out following the line × tester mating design outlined by Kempthorne [7] and further elaborated by Arunachalam [8]. In the present experiment, 34 male parents were crossed with the four CMS lines in line × tester matting design to obtain 136 cross combinations. Estimation of general combining ability (gca) and specific combining ability (sca) variances and effects was carried out using the observations taken in F_1 generation of the line × tester set of crosses [9].

3. RESULTS AND DISCUSSION

Analysis of variance (ANOVA) revealed the existence of significant differences among the genotypes, revealing that sufficient variability is present for different traits (Table 1). The perusal of the data on combining ability variances revealed that the magnitude of additive genetic variance (σ^2A) was observed to be lower than dominance genetic variance (σ^2D) for all the traits *viz.,* days to 50 per cent flowering, plant height, flag leaf area, number of effective tillers $plant^{-1}$, panicle length, number of spikelets $panicle^{-1}$, test weight, grain yield, biological yield, harvest index, kernel length and kernel breadth, indicating the predominance of non-additive gene action (Table 2).

For days to 50 percent flowering and kernel breadth, negative values of combining ability are generally considered to be desirable; while for rest of the traits, positive estimates of combining ability effects are usually preferable [5]. The estimates of GCA effect for different agro-morphological traits revealed that the significant negative GCA effect in CMS lines for days to 50% flowering was exhibited by SKUA-7A (Table 3). Within pollen parents, the highest significant desirable GCA effect for days to 50% flowering was revealed by SKUA-420 followed by SKUA-415, SKUA-497 and RL-10. SKUA-21A × RL-9 showed highest significant desirable negative value of SCA effect for days to 50% flowering (Table 4). Among the female parents, SKUA-7A recorded significant positive GCA effect for plant height. Among the male parents, RL-10, SKUA-496 and SKUA-497 recorded significant and highest positive value of GCA effect for plant height. The cross combination SKUA-19A × RL-1 recorded significant and highest positive SCA effect for plant height. The significantly positive value of GCA effect for flag leaf area amongst the CMS lines was observed in SKUA-7A and in male parents the highest significant positive value was observed in RL-10 followed by RL-11. The cross combination, SKUA-19A × RL-1 recorded the highest significant desirable estimate of SCA effect for flag leaf area.

The significant positive value of GCA effect for number of effective tillers plant^{-1} amongst the female parents was observed in SKUA-7A. Whereas, amongst the male parents, the highest significant positive GCA effect was observed in SKUA-497 followed by SKUA-420 and SKUA-496. The cross combination, SKUA-19 × RL-1 followed by SKUA-19A × SKUA-496 recorded the highest significant desirable estimate of SCA effect for number of effective tillers plant^{-1}. None of the female parent showed significant positive value of GCA effect for panicle length; while among the male parents, maximum significant positive value of GCA effect was observed in SKUA-497 followed by SKUA-496. The cross combinations, SKUA-19A × Pusa Sugandh-3 and SKUA-19A × RL-13 recorded similar but maximum significant desirable estimate of SCA effect for panicle length. The significant and positive GCA effect for number of spikelet panicle^{-1} amongst the female parents was observed in SKUA-7A. While amongst, the male parents maximum significant positive value of GCA effect was observed in SKUA-497 followed by RL-10 and SKUA-420. The cross combination SKUA-19A × RL-13 followed by SKUA-19A × RL-13 recorded maximum significant desirable estimate of SCA effect for number of spikelets panicle^{-1}. The significant desirable value of GCA effect for test weight among the female parents was observed in SKUA-11A; whereas among the male parents, maximum significant positive value of GCA effect was observed in RL-4 followed by RL-5. For test weight, highest significant desirable value of SCA effect was recorded by SKUA-21A × RL-14 followed by SKUA-11A × RL-4 and SKUA 7A × SKUA-412.

Amongst the female parents, significant positive GCA effect for grain yield was observed for SKUA-7A, while amongst the male parents, highest significant positive value of GCA effect was observed for SKUA-420 followed by SKUA-497 and RL-10. The cross combination SKUA-19 × RL-13 revealed highest significant positive value of SCA effect for grain yield followed by SKUA-19A × RL-1, SKUA-7A × RL3 and SKUA-11A × RL-4. Amongst the female parents, significant positive value of GCA effect for biological yield was observed for SKUA-7A followed by SKUA-19A. Amongst the male parents, SKUA-420 depicted maximum significant positive value of GCA effect. The cross combination SKUA- 19A × RL-1 revealed the highest significant positive value of SCA effect for biological yield. Amongst the female and male parents, significant positive value of GCA effect for harvest index was observed by SKUA-11A and RL-11, respectively. The cross combination SKUA-19A × SKUA-403 revealed the highest significant positive value of SCA effect for harvest index followed by SKUA-19A × Pusa Basmati-1509.

Among the female parents, SKUA-7A recorded significant positive estimate of GCA effect for kernel length. Highest significant desirable GCA effect for the trait amongst the male parents was observed in RL-7 followed by Pusa Basmati-1509. Amongst the crosses, SKUA-21A × Pusa Basmati-1509 recorded the highest significant positive SCA effect for kernel length followed by SKUA-7A × RL-9. For kernel breadth, the CMS lines SKUA-11A and SKUA-21A recorded significant negative values of GCA effect. Among the pollen parents, significant desirable value of GCA effect was revealed by RL-9 followed by SKUA-486. Cross combination SKUA-19A × SKUA-412 recorded highest significant desirable value of SCA effect for kernel breadth.

Table 1. Analysis of variance for combining ability of different characters

S. No.	Characters	Mean squares						
		Replications (d.f.=2)	Crosses (d.f.=135)	Females (d.f.=3)	Males (d.f.=33)	Female × male (d.f.=99)	Error (d.f.=270)	Total (d.f.=407)
1.	Days to 50% flowering	4.43**	40.75 **	6.44 **	78.43**	29.23**	0.35	13.77
2.	Plant height (cm)	97.03**	140.45 **	37.46	313.95 **	85.80 **	4.09	49.74
3.	Flag leaf area (cm^2)	5.00**	25.63 **	8.81*	50.01 **	18.02 **	0.33	8.75
4.	Number of tillers $plant^{-1}$	3.63*	18.52 **	65.19*	32.56 **	14.24 **	1.12	6.90
5.	Panicle length (cm)	0.04	3.63 **	0.72	7.03 **	2.59 **	0.33	1.43
6.	Number of spikelets $panicle^{-1}$	0.26	1342.80 **	473.40	2992.85 **	819.14 **	7.18	450.17
7.	1000 grain weight (g)	0.25	5.87 **	11.25**	7.79	5.07 **	0.16	2.06
8.	Grain yield (tha^{-1})	0.53**	15.38 **	6.54**	34.08 **	9.41 **	0.05	5.14
9.	Biological yield (tha^{-1})	0.03	77.68 **	39.20**	161.22 **	51.00 **	0.09	25.83
10.	Harvest Index (%)	44.29**	58.54 **	24.89**	81.44 *	51.93 **	3.44	21.92
11.	Kernel length (mm)	0.02	0.45**	0.12	0.20	0.37 **	0.01	0.16
12.	Kernel breadth (mm)	0.003	0.04 **	0.09	0.035	0.04 **	0.004	0.02

**, ** = Significant at 0.05 and 0.01 levels, respectively; d.f. = degree of freedom*

Table 2. Estimates of combining ability and genetic component of variances for various agro-morphological and physiochemical traits

S. No	Character	σ^2GCA	σ^2SCA	σ^2A	σ^2D	σ^2A/ σ^2D
1	Days to 50 percent flowering	0.23	9.62	0.46	9.62	0.01
2	Plant height (cm)	1.58	27.26	3.15	27.26	0.12
3	Flag leaf area (cm^2)	0.19	5.89	0.39	5.89	0.07
4	Number of tillers $plant^{-1}$	0.08	4.38	0.16	4.38	0.03
5	Panicle length (cm)	0.02	0.76	0.05	0.76	0.06
6	Number of spikelets $panicle^{-1}$	30.25	270.16	32.07	270.16	0.12
7	Grain yield ($t\ ha^{-1}$)	0.19	3.12	0.38	3.12	0.12
8	Biological yield ($t\ ha^{-1}$)	0.86	16.97	1.73	16.97	0.10
9	Harvest Index (%)	0.02	16.17	0.04	16.17	0.003
10	Test weight (g)	0.08	1.64	0.16	1.64	0.09
11	Kernel length (mm)	0.01 1	0.12	0.003	0.12	0.02
12	Kernel breadth (mm)	0.0004	0.01	0.0009	0.01	0.08

Table 3. Estimates of general combining ability (GCA) effects of parents for various agro-morphological and physiochemical traits

Cross combinations	Days to 50% flowering	Plant height	Flag leaf area	Number of tillers per plant	Panicle length	Number of spikelets per panicle	1000 Grain weight	Grain yield	Biological yield	Harvest index	Kernel length	Kernel breadth
Female parents												
SKUA-7A	-0.363**	0.822**	0.272 **	0.227*	0.036	3.154**	-0.373**	0.327**	0.837**	-0.268	0.046 **	0.017 **
SKUA-11A	0.216 **	-0.554**	-0.418**	-0.017	-0.112*	-1.711**	0.083*	-0.044*	-0.389**	0.731**	-0.036 **	-0.034 **
SKUA-19A	0.059	-0.338	0.069	0.093	0.085	-0.771**	-0.122**	0.005	0.093**	-0.133	-0.012	0.031 **
SKUA-21A	0.088	0.070	0.077	-0.303**	-0.010	-0.673*	0.412**	-0.288**	-0.541**	-0.330	0.002	-0.014 *
Male parents												
RL-1	-1.613 **	4.269 **	3.367 **	1.818**	0.773 **	9.900**	0.314**	2.137 **	5.076 **	1.662 **	0.105 **	0.137 **
RL-2	-1.029 **	3.706 **	3.248 **	1.055**	0.336 *	12.200**	0.768 **	2.235 **	4.508 **	2.547 **	0.303 **	0.096 **
RL-3	3.750 **	1.751 **	-1.058**	-0.145	-0.027	0.554 **	-0.044	0.600**	0.201 *	0.661	0.062	-0.029
RL-4	2.637 **	-1.919 **	-2.751 **	-1.432**	-0.339 *	-11.525 **	1.617 **	1.071 **	-3.381 **	2.649 **	0.270 **	0.054 **
RL-5	2.721 **	-6.756 **	-1.650 **	-2.007 **	-0.897 **	-19.975 **	1.161 **	-1.425 **	-3.791 **	2.850 **	0.170 **	-0.054 **
RL-6	3.554 **	-7.931 **	-0.604 **	-2.624 **	-0.502 **	-4.787 **	0.351 **	-2.407 **	-5.107 **	0.375	-0.172 **	-0.013
RL-7	3.137 **	-6.856 **	-2.500 **	-1.907 **	-0.339 *	-15.475 **	0.618 **	-1.923 **	-3.420 **	-4.575 **	0.462 **	-0.029
RL-8	0.637**	-0.144	0.749 **	-0.052	-0.227	2.938 **	0.224 *	-0.580 **	-1.126 **	-0.459	-0.097 **	-0.013
RL-9	1.554 **	2.369 **	-1.178 **	-0.057	0.211	6.163 **	0.268 *	0.593 **	0.843 **	2.160 **	0.020	-0.088 **
RL-10	-3.113 **	9.894 **	4.478 **	2.880 **	0.848 **	30.433 **	-0.351 **	2.868 **	6.706 **	-0.583	-0.363 **	0.004
RL-11	-1.029 **	4.319 **	3.410 **	0.918 **	0.693 **	10.354 **	0.156	1.605 **	2.268 **	4.546 **	0.180 **	0.037 *
RL-12	0.637 **	0.194	-0.306	-0.845 **	0.148	-1.975 *	0.655 **	0.133 *	0.077	1.101 *	-0.163 **	-0.013
RL-13	3.137 **	-8.131 **	-2.826 **	-2.057 **	-1.102 **	-16.925 **	0.474 **	1.357 **	-3.072 **	-0.242	-0.405 **	0.012
RL-14	2.637 **	-6.431 **	-1.188 **	-1.282 **	-0.832 **	-19.725 **	0.405 **	-1.517 **	-3.415 **	-0.364	-0.338 **	-0.054 **
SKUA-403	3.304 **	-1.856 **	-3.209 **	-1.932 **	-1.105 **	-29.950 **	0.899 **	-1.476 **	-3.880 **	2.548 **	-0.280 **	0.021
SKUA-408	0.054	-0.156	-1.831 **	-0.782 *	-0.014	-2.125 *	-1.183 **	-1.357 **	-1.811 **	-5.228 **	-0.022	-0.063 **
SKUA-412	3.221 **	-2.881 **	-0.982 **	-0.407	-0.302	-1.250	1.042 **	-0.859 **	-1.285 **	-2.199 **	-0.172 **	0.021
SKUA-415	-2.446 **	1.894 **	1.944 **	2.243 **	0.748 **	19.925 **	-1.582 **	2.031 **	5.091 **	-2.061 **	0.003	-0.021
SKUA-420	-4.946 **	8.156 **	3.124 **	3.068 **	0.923 **	29.375 **	0.650 **	3.643 **	8.681 **	-0.933	0.370 **	0.012
SKUA-483	-4.446 **	4.094 **	0.377 *	0.043	0.236	12.763 **	0.591 **	1.025 **	0.202 *	7.208 **	-0.022	0.004
SKUA-484	-0.779 **	1.694 **	0.329	-0.545	0.348 *	2.900 **	-1.122 **	-0.055	-0.245 **	-0.115	-0.130 **	-0.004
SKUA-486	0.554 **	-1.431 *	0.216	-0.227	0.373 *	-6.350 **	0.211 *	-1.127 **	-1.804 **	-3.019 **	0.020	-0.079 **
SKUA-487	2.304 **	-2.806 **	0.716 **	-0.245	0.086	-10.250 **	-0.008	-1.062 **	-1.642 **	-3.024 **	-0.138 **	-0.013
SKUA-488	1.221 **	-1.056	0.374 *	-0.807 **	0.198	-12.350 **	-0.064	-0.915 **	-1.644 **	-1.712 **	-0.272 **	-0.021
SKUA-491	0.887 **	0.819	0.682 **	-0.257	0.048	-9.212 **	0.192	-0.896 **	-1.882 **	-0.555	-0.105 **	0.021
SKUA-494	-2.446 **	2.419 **	0.467 **	0.930 **	0.698 **	15.150 **	-1.207 **	1.610 **	3.461 **	0.215	0.562 **	0.071 **
SKUA-495	-2.863 **	1.044	-0.342 *	-0.282	0.273	1.150	0.230 *	0.080	-0.403 **	1.705 **	0.112 **	0.029
SKUA-496	-5.113 **	10.181 **	1.957 **	3.043 **	1.348 **	25.438 **	-1.320 **	2.635 **	5.868 **	-0.009	0.320 **	0.029
SKUA-497	-3.113 **	9.069 **	2.199 **	3.893 **	1.398 **	31.725 **	0.899 **	2.933 **	5.683 **	1.916 **	-0.005	0.154 **
SKUA-498	2.721 **	-0.181	-0.739 **	0.293	-0.052	-4.150 **	0.255 *	-0.977 **	-1.448 **	-3.038 **	-0.272 **	0.046 *
SKUA-499	-0.529 **	-6.756 **	-1.477 **	-1.807 **	-1.477 **	-11.537 **	-0.127	-1.553 **	-2.861 **	-3.582 **	-0.172 **	-0.013
SKUA-500	0.804 **	-2.456 **	-1.046 **	-1.070 **	-0.602 **	-9.625 **	-0.933 **	-1.449 **	-3.428 **	1.337 *	0.220 **	-0.029
Pusa Sugandh-3	-0.446 *	-8.994 **	-3.441 **	-0.857 **	-2.027 **	-23.675 **	-0.938 **	-2.157 **	-4.781 **	-0.040	0.095 **	-0.021
Pusa Basmati-1509	-2.363 **	0.869	-0.506 **	1.443 **	0.148	-3.300 **	-1.176 **	0.579 **	1.765 **	-1.746 **	0.428 **	-0.046 *

**, ** = Significant at 0.05 and 0.01 levels, respectively*

Table 4. Estimates of specific combining ability (SCA) effects for various agro-morphological and physiochemical traits of different cross combinations

Cross combinations	Days to 50% flowering	Plant height	Flag leaf area	Number of tillers per plant	Panicle length	Number of spikelets per panicle	1000 Grain weight	Grain yield	Biological yield	Harvest index	Kernel length	Kernel breadth
SKUA-7A × RL-1	2.946**	-14.972**	-7.256**	-4.427**	-0.911**	-18.904**	-0.671**	-4.642**	-11.741**	4.881**	0.137	-0.075*
SKUA-11A × RL-1	-2.299**	5.804**	1.480**	1.517*	0.737*	11.461**	0.373	1.826**	4.568**	-3.491**	-0.048	0.175**
SKUA-19A × RL-1	-3.142**	12.938**	7.177**	5.307**	1.890**	36.521**	1.704**	3.737**	11.677**	-7.243**	-0.271**	-0.023
SKUA-21Ax RL-1	2.495**	-3.770**	-1.401**	-2.397**	-1.715**	-29.077**	-1.406**	-0.920**	-4.503**	5.853**	0.182*	-0.077*
SKUA-7A × RL-2	-2.696**	2.241*	1.140**	2.065**	1.224*	3.704*	0.824**	0.369**	2.106**	4.357**	0.196**	0.100**
SKUA-11A × RL-2	-1.882**	1.866	-3.331**	-1.421*	-0.626	-16.639**	-0.359	-2.272**	-6.845**	8.174**	-0.456**	-0.116**
SKUA-19A × RL-2	-4.725**	2.451*	2.353**	1.070	0.727*	14.221**	0.173	1.628**	4.324**	-3.072**	-0.013	0.186**
SKUA-21A × RL-2	5.912**	-4.558**	1.118**	0.416	0.122	6.123**	-0.638**	0.275*	0.414*	-0.745	0.273**	-0.169**
SKUA-7A × RL-3	-2.221**	3.554**	4.034**	2.876**	0.889**	24.054**	1.010**	3.565**	3.204**	2.525*	0.296**	0.142**
SKUA-11A × RL-3	1.534**	-0.051	4.368**	0.529	-0.063	6.611**	-0.246	0.823**	1.182**	1.453	0.186*	-0.025
SKUA-19A × RL-3	-3.642**	3.457**	-2.118**	1.470*	0.190	10.871**	-1.165**	1.794**	5.801**	-5.239**	0.362**	-0.056
SKUA-21A × RL-3	2.328**	0.148	-2.129**	-1.984**	-1.015**	-6.427**	0.401	-1.053**	-3.779**	6.311**	-0.252**	0.123**
SKUA-7A × RL-4	0.029	-0.884	-0.801*	1.123	0.001	14.721**	-0.802**	1.686**	2.139**	6.871**	0.096	0.075*
SKUA-11A × RL-4	-2.882**	9.641**	4.208**	2.867**	0.799*	25.886**	2.742**	3.094**	5.925**	3.523**	0.044	0.092*
SKUA-19A × RL-4	1.275**	-5.024**	-1.595**	-2.343**	0.002	-18.054**	-1.253**	-2.142**	-2.937**	-9.333**	0.120	-0.073*
SKUA-21A × RL-4	1.578**	-3.733**	-1.813**	-1.647**	-0.803*	-22.552**	-0.687**	-2.638**	-5.127**	-1.060	-0.260**	-0.094**
SKUA-7A × RL-5	-0.054	-0.747	1.150**	0.298	-0.140	-5.929**	-0.069	0.940**	0.799**	5.099**	-0.004	0.050
SKUA-11A × RL-5	-1.368**	2.129*	1.813**	1.458*	0.842**	7.164**	1.298**	0.488**	0.815**	8.613**	0.189*	0.067
SKUA-19A × RL-5	-1.475**	-6.587**	1.740**	1.868**	0.727*	6.204**	1.103**	0.878**	1.730**	4.018**	0.254**	0.131**
SKUA-21A × RL-5	0.162	7.205**	2.402**	2.028**	0.855**	19.298**	-1.331**	0.426**	0.117	4.531**	-0.160*	0.014
SKUA-7A × RL-6	1.779**	8.628**	3.541**	0.114	0.364	8.783**	0.442*	1.828**	5.351**	-5.576**	0.171*	0.075*
SKUA-11A × RL-6	-0.466	-8.096**	-3.656**	-0.641	-0.138	-25.452**	-0.391	-2.930**	-6.540**	-1.131	0.019	-0.008
SKUA-19A × RL-6	-2.642**	5.088**	-0.862*	1.549*	0.515	13.208**	0.233	2.014**	4.236**	-0.630	-0.171*	-0.073*
SKUA-21A × RL-6	1.328**	-5.620**	0.977**	-1.022	-0.740*	3.461*	-0.284	-0.913**	-3.047**	7.336**	-0.018	0.006
SKUA-7A × RL-7	-1.471**	5.953**	4.287**	2.898**	1.251**	16.571**	0.436*	1.294**	2.855**	2.451*	0.296**	-0.042
SKUA-11A × RL-7	-1.382**	11.429**	3.073**	2.842**	1.049**	23.336**	0.438*	2.049**	5.570**	2.171*	0.686**	0.125**
SKUA-19A × RL-7	0.108	-9.687**	-2.246**	-3.568**	-0.798*	-21.704**	0.016	-1.713**	-4.391**	0.833	-0.338**	0.111**
SKUA-21A × RL-7	1.745**	-7.695**	-1.968**	-2.172**	-0.503	-18.202**	0.382	-1.630**	-4.034**	-1.114	-0.052	0.056
SKUA-7A × RL-8	2.029**	0.141	2.039**	-0.637	-0.261	-8.042**	-0.908**	-1.018**	-1.926**	-2.028	0.062	-0.059
SKUA-11A × RL-8	0.118	0.766	-0.168	1.487*	0.687*	1.573	-0.865**	0.593**	2.036**	-2.390*	-0.056	-0.008

Table 4. Continued…

Cross combinations	Days to 50% flowering	Plant height	Flag leaf area	Number of tillers per plant	Panicle length	Number of spikelets per panicle	1000 Grain weight	Grain yield	Biological yield	Harvest index	Kernel length	Kernel breadth
SKUA-21A × RL-8	1.578**	-2.608*	-0.883*	-1.427*	-0.415	5.886**	-0.794**	0.961**	2.282**	-0.669	-0.227**	-0.061
SKUA-7A × RL-9	-0.221	5.228**	-2.391**	-1.252*	0.601	-0.317	2.524**	-0.972**	-3.665**	5.967**	1.046**	-0.084*
SKUA-11A × RL-9	7.201**	-7.896**	-1.572**	-0.708	0.349	-9.302**	-0.309	-0.827**	-1.963**	0.618	0.094	-0.100**
SKUA-19A × RL-9	-0.642	-2.212	0.662	-0.318	-1.098**	-17.142**	-1.954**	-0.749**	-0.694**	-4.124**	-0.530**	0.136**
SKUA-21A × RL-9	-6.338**	4.880**	3.301**	2.278**	0.147	26.761**	0461*	2.547**	6.323**	2.461*	0.610**	0.248**
SKUA-7A × RL-10	0.446	-3.847**	-2.530**	-1.390*	-0.836*	-8.837**	0.817**	-0.467**	-0.518**	-1.297	-0.271**	-0.075*
SKUA-11A × RL-10	-1.132**	1.479	-0.041	-1.496*	0.312	5.928**	-2.240**	-0.972**	-1.322**	-2.359*	-0.223**	-0.191**
SKUA-19A × RL-10	-0.642	1.213	1.956**	4.345**	0.115	8.588**	-0.135	1.116**	3.183**	-1.472	0.120	0.311**
SKUA-21A × RL-10	1.328**	1.155	0.615	-1.459*	0.410	-5.679**	1.558**	0.322*	-1.343**	5.128**	0.373**	-0.044
SKUA-7A × RL-11	-2.304**	3.278**	4.867**	1.073	0.920**	18.141**	0.437*	2.120**	3.996**	0.170	-0.054	0.258**
SKUA-11A × RL-11	0.118	-3.946**	-0.053	-0.083	0.068	-9.754**	1.804**	0.422**	-0.015	2.618*	0.227**	-0.058
SKUA-19A × RL-11	0.941**	-2.862*	-4.090**	-2.293**	-1.029**	-22.634**	-1.265**	-3.068**	-6.949**	2.983**	0.204**	-0.123**
SKUA-21A × RL-11	-1.245**	3.530**	0.724*	1.303*	1.042**	14.246**	0.975**	0.526**	2.968**	5.771**	0.377**	0.077*
SKUA-7A × RL-12	-2.971**	6.003**	3.727**	1.935**	-0.336	10.171**	-0.739**	1.652**	5.837**	-5.608**	0.296**	-0.059
SKUA-11A × RL-12	-1.549**	0.679	-2.447**	-0.621	0.112	3.136	-0.095	0.590**	-0.177	5.537**	-0.189**	-0.008
SKUA-19A × RL-12	9.275**	-11.437**	-4.110**	-1.980**	-1.385**	-23.404**	-0.491*	-3.386**	-7.198**	-2.786**	-0.413**	0.094**
SKUA-21A × RL-12	-4.755**	4.755**	2.829**	1.666**	1.610**	10.098**	1.325**	1.144**	1.538**	2.857**	0.307**	-0.027
SKUA-7A × RL-13	1.529**	-9.472**	-2.094**	-2.952**	-1.386**	-20.879**	-0.508*	-3.168**	-6.730**	-4.868**	-0.096	-0.117**
SKUA-11A × RL-13	-0.382	-3.596**	-1.324**	-1.708**	-1.338**	-18.614**	-0.065	-2.260**	-5.118**	3.773**	0.186*	0.034
SKUA-19A × RL-13	-1.892**	8.688**	2.449**	3.782**	2.165**	41.646**	0.090	3.894**	8.324**	1.144	-0.305**	0.036
SKUA-21A × RL-13	0.745*	4.380**	0.968**	0.878	0.560	-2.152	0.483*	1.534**	3.524**	-0.049	0.215**	0.048
SKUA-7A × RL-14	0.029	4.928**	1.465**	0.173	1.145**	12.921**	-1.439**	0.218	0.200	1.500	0.871**	-0.150**
SKUA-11A × RL-14	-1.549**	-4.096**	-1.585**	1.317*	-0.007	15.486**	-0.445*	0.263*	0.885**	-0.392	0.186*	0.100**
SKUA-19A × RL-14	-1.275**	2.912*	1.931**	3.593**	1.428**	-21.654**	-1.091**	-1.329**	-2.083**	-5.594**	-0.738**	0.036
SKUA-21A × RL-14	1.245**	2.080	2.051**	2.103**	1.290**	6.752**	2.975**	0.847**	0.998**	4.486**	0.318**	0.014
SKUA-7A × SKUA-403	0.029	-5.147**	-1.774**	-3.077**	-1.096**	-21.254**	-0.983**	-2.462**	-4.832**	-4.142**	-0.354**	0.075*
SKUA-11A × SKUA-403	1.451**	2.129	-0.491	1.067	0.365	-8.889**	-0.940**	0.423**	2.284**	-5.370**	0.161*	-0.041
SKUA-19A × SKUA-403	-1.059**	0.913	0.193	-0.343	0.268	10.871**	0.765**	1.183**	0.542**	10.134**	0.237**	0.061
SKUA-21A × SKUA-403	-0.422	2.105	2.072**	2.353**	0.463	19.273**	1.158**	0.857**	2.006**	-0.623	-0.043	-0.094**
SKUA-7A × SKUA-408	0.279	-0.147	1.499**	-0.727	0.176	-4.679**	-2.702**	-0.102	-0.485**	1.071	-0.379**	-0.009
SKUA-11A × SKUA-408	1.034**	-0.371	-0.138	-1.183	0.274	-11.114**	1.242**	0.250*	1.295**	-1.951	-0.064	0.042
SKUA-19A × SKUA-408	1.858**	3.613**	-0.178	-0.193	-0.323	4.046*	0.597**	0.274*	-0.397*	3.967**	0.612**	-0.056
SKUA-21A × SKUA-408	-3.172**	-3.095**	-1.183**	2.103**	-0.128	11.748**	0.863**	-0.423**	-0.413*	-3.087**	-0.168*	0.023
SKUA-7A × SKUA-412	-1.887**	0.978	-0.460	-0.502	0.214	-1.954	2.123**	0.880**	2.470**	-1.382	0.071	0.341**
SKUA-11A × SKUA-412	0.534	4.454**	2.403**	-0.558	0.512	-4.289*	-0.783**	-0.225	-0.421*	-0.463	0.252**	-0.041

Table 4. Continued…

Cross combinations	Days to 50% flowering	Plant height	Flag leaf area	Number of tillers per plant	Panicle length	Number of spikelets per panicle	1000 Grain weight	Grain yield	Biological yield	Harvest index	Kernel length	Kernel breadth
SKUA-19A × SKUA-412	0.691	0.038	-1.597**	-0.268	-1.035**	8.171**	-0.328	-0.714**	-2.766**	4.584**	-0.238**	-0.239**
SKUA-21A × SKUA-412	0.662	-5.470**	-0.345	1.328*	0.310	-1.927	-1.012**	0.059	0.718**	-2.739*	-0.085	-0.061
SKUA-7A × SKUA-415	-1.887**	4.803**	1.536**	0.548	0.864**	11.071**	-0.876**	1.333**	1.994**	2.984**	0.096	-0.050
SKUA-11A × SKUA-415	-3.799**	-4.821**	-0.074	0.492	-0.288	5.836**	0.591**	0.805**	2.623**	-1.184	0.077	0.034
SKUA-19A × SKUA-415	-0.642	3.963**	-0.654	0.882	-0.485	9.996**	-1.127**	0.792**	0.538**	3.583**	0.020	0.036
SKUA-21A × SKUA-415	6.328**	-3.945**	-0.808*	-1.922**	-0.090	-26.902**	1.412**	-2.931**	-5.155**	-5.384**	-0.193**	-0.019
SKUA-7A × SKUA-420	0.279	0.841	3.096**	3.773**	0.389	2.921	1.552**	1.928**	6.013**	-2.604*	0.163*	-0.084*
SKUA-11A × SKUA-420	-0.299	4.816**	0.466	-0.533	-0.063	-0.014	1.410**	0.163	-1.338**	3.491**	-0.123	0.134**
SKUA-19A × SKUA-420	1.191**	-0.099	-1.194**	-1.493*	0.040	-0.554	0.081	-1.729**	-3.829**	-0.712	0.254**	-0.031
SKUA-21A × SKUA-420	-1.172**	-5.558**	-2.368**	-1.747**	-0.365	-2.352	-3.043**	-0.363**	-0.846**	-0.175	-0.293**	-0.019
SKUA-7A × SKUA-483	0.113	4.403**	-1.456**	0.648	1.126**	13.533**	1.654**	0.347**	0.882**	-1.232	0.021	-0.042
SKUA-11A × SKUA-483	-0.799*	-1.021	1.183**	0.492	0.024	14.998**	-1.605**	0.678**	1.038**	1.520	0.136	-0.025
SKUA-19A × SKUA-483	-0.642	-2.437*	-0.473	-0.618	-0.573	-27.292**	-1.577**	-0.091	-1.120**	3.968**	0.279**	0.011
SKUA-21A × SKUA-483	1.328**	-0.945	0.746*	-0.522	-0.578	-1.239	1.529**	-0.934**	-0.800**	-4.256**	-0.435**	0.056
SKUA-7A × SKUA-484	-1.887**	5.803**	0.002	1.635**	0.564	17.296**	-0.386	1.739**	1.970**	6.045**	-0.504**	0.000
SKUA-11A × SKUA-484	-3.466**	-0.821	-2.762**	0.679	-0.088	-2.639	-1.669**	-0.049	0.405*	-1.073	0.311**	-0.016
SKUA-19A × SKUA-484	4.691**	-4.037**	3.215**	-1.030	-0.285	-7.179**	1.513**	-1.032**	-1.223**	-4.049**	0.254**	0.052
SKUA-21A × SKUA-484	0.662	-0.945	-0.456	-1.284*	-0.190	-7.477**	0.542*	-0.658**	-1.152**	-0.923	-0.060	-0.036
SKUA-7A × SKUA-486	0.779*	-1.072	-0.895**	1.118	0.739*	-1.954	0.354	-0.382**	-0.228	-2.532*	-0.088	-0.059
SKUA-11A × SKUA-486	-0.799*	-1.696	1.191**	-1.118	-0.313	1.211	0.175	0.173	0.528**	-0.150	-0.039	0.025
SKUA-19A × SKUA-486	-2.309**	1.088	0.044	-0.648	-0.710*	0.271	-0.147	0.041	-0.677**	2.904**	0.170*	-0.173**
SKUA-21A × SKUA-486	2.328**	1.680	-0.340	0.648	0.285	0.473	-0.381	0.167	0.377*	-0.223	-0.043	0.206**
SKUA-7A × SKUA-487	-0.971**	1.803	-0.885*	0.335	0.176	-8.854**	0.673**	-0.397**	-0.230	-2.643*	-0.129	-0.059
SKUA-11A × SKUA-487	-0.549	2.179	1.791**	-0.421	-0.226	9.911**	0.017	0.058	0.642**	-1.635	0.152*	-0.008
SKUA-19A × SKUA-487	0.608	-0.037	-0.952**	-0.530	0.077	0.871	-0.128	0.086	-0.489**	2.516*	-0.038	-0.073*
SKUA-21A × SKUA-487	0.912*	-3.945**	0.047	0.616	-0.028	-1.927	-0.562**	0.252*	0.078	1.762	0.015	0.139**
SKUA-7A × SKUA-488	3.113**	-4.947**	-0.873*	-0.902	-0.286	0.846	0.379	-0.371**	-0.978**	0.405	-0.096	0.083*
SKUA-11A × SKUA-488	-1.466**	-0.571	0.183	0.042	0.062	1.711	0.000	-0.062	0.155	-0.790	0.052	-0.100**
SKUA-19A × SKUA-488	-0.309	2.713*	1.230**	1.132	-0.035	-6.229**	0.078	0.012	-0.307	1.138	0.029	-0.064
SKUA-21A × SKUA-488	-1.338**	2.805*	-0.541	-0.272	0.260	3.673*	-0.456*	0.422**	1.130**	-0.753	0.015	0.081*
SKUA-7A × SKUA-491	0.446	-1.322	-1.081**	0.548	0.064	-0.592	0.423*	-0.279*	-1.000**	1.364	0.238**	0.041
SKUA-11A × SKUA-491	-1.799**	1.054	0.788*	0.292	0.012	4.923**	-0.183	0.003	0.315	-0.868	-0.248**	-0.041
SKUA-19A × SKUA-491	2.358**	-0.162	0.512	0.182	-0.085	-5.367**	0.072	0.063	0.471**	-1.523	0.095	-0.106**
SKUA-21A × SKUA-491	-1.005**	0.430	-0.219	-1.022	0.010	1.036	-0.312	0.213	0.214	1.026	-0.085	0.106**
SKUA-7A × SKUA-494	-1.221**	2.378*	0.864*	3.860**	0.014	11.146**	-2.378**	1.315**	2.467**	1.148	0.004	-0.034

Table 4. Continued…

Cross combinations	Days to 50% flowering	Plant height	Flag leaf area	Number of tillers per plant	Panicle length	Number of spikelets per panicle	1000 Grain weight	Grain yield	Biological yield	Harvest index	Kernel length	Kernel breadth
SKUA-11A × SKUA-494	8.201**	-0.546	-2.890**	0.004	0.562	8.911**	1.443**	0.493**	0.630**	1.443	0.486**	-0.083*
SKUA-19A × SKUA-494	-3.309**	-4.662**	-0.593	-4.405**	-1.235**	-16.729**	0.871**	-1.466**	-3.258**	-0.057	-0.405**	0.086*
SKUA-21A × SKUA-494	-3.672**	2.830*	2.619**	0.541	0.660*	-3.327	0.064	-0.343**	0.162	-2.534*	-0.085	0.031
SKUA-7A × SKUA-495	4.529**	-4.947**	-1.977**	-0.627	-0.561	-18.654**	-1.114**	-1.656**	-3.730**	0.898	0.021	0.066
SKUA-7A × SKUA-496	0.951**	0.329	1.753**	1.517*	0.987**	20.411**	1.180**	1.886**	3.113**	3.433**	-0.198**	-0.050
SKUA-11A × SKUA-495	-1.225**	-3.387**	0.606	-1.693**	-0.410	-6.729**	-0.616**	-1.437**	-2.168**	-4.083**	-0.155*	-0.114**
SKUA-19A × SKUA-495	-4.255**	8.005**	-0.382	0.803	-0.015	4.973**	0.550**	1.207**	2.785**	-0.247	0.332**	0.098**
SKUA-21A × SKUA-495	-1.221**	-2.284*	-0.616	-2.152**	-0.636	-20.342**	1.136**	-1.024**	-1.824**	-1.215	0.046	-0.134**
SKUA-11A × SKUA-496	1.868**	1.441	0.120	-1.708**	-0.088	-2.127	-1.420**	-0.922**	-2.535**	1.497	-0.006	-0.016
SKUA-19A × SKUA-496	-0.642	2.476*	2.867**	5.282**	0.615	12.983**	0.734**	2.142**	4.181**	1.174	-0.163*	0.119**
SKUA-21A × SKUA-496	-0.005	-1.633	-2.371**	-1.422*	0.110	9.486**	-0.450*	-0.195	0.178	-1.456	0.123	0.031
SKUA-7A × SKUA-497	-0.554	0.828	1.219**	0.298	-0.286	-5.129**	0.517*	0.608**	-0.779**	5.383**	-0.429**	-0.025
SKUA-11A × SKUA-497	-1.799**	3.804**	2.112**	3.442**	0.362	3.836*	0.260	1.290**	1.490**	3.195**	-0.481**	0.259**
SKUA-19A × SKUA-497	4.025**	-8.412**	-3.765**	-3.868**	-1.335**	-9.904**	-0.508*	-3.066**	-5.291**	-4.511**	0.529**	-0.039
SKUA-21A × SKUA-497	-1.672**	3.780**	0.434	0.128	1.260**	11.198**	-0.269	1.167**	4.579**	-4.068**	0.382**	-0.194**
SKUA-7A × SKUA-498	1.613**	-0.322	-0.260	0.598	-0.336	-1.854	0.411	-0.398**	-0.495**	-1.619	0.037	0.016
SKUA-11A × SKUA-498	-0.966**	0.554	-0.861*	0.242	0.312	-2.989	-0.095	-0.077	0.221	-1.204	0.052	0.067
SKUA-19A × SKUA-498	1.191**	1.438	0.729*	0.032	-0.085	-0.979	0.209	0.181	-0.330	2.717*	-0.038	0.002
SKUA-21A × SKUA-498	-1.838**	-1.670	0.392	-0.872	0.110	5.823**	-0.525*	0.294*	0.603**	0.106	-0.052	-0.086*
SKUA-7A × SKUA-499	-4.137**	-1.647	-0.575	1.198*	1.289**	27.733**	-1.131**	1.914**	4.279**	1.608	-0.063	-0.059
SKUA-11A × SKUA-499	-4.382**	-3.671**	1.068**	-0.158	-0.963**	0.748	1.083**	0.289*	1.761**	-3.040**	-0.181*	-0.008
SKUA-19A × SKUA-499	3.775**	7.013**	2.618**	1.232*	1.440**	5.258**	0.191	0.707**	0.903**	3.534**	-0.005	0.027
SKUA-21A × SKUA-499	4.745**	-1.695	-3.110**	-2.272**	-1.765**	-33.739**	-0.143	-2.910**	-6.943**	-2.103*	0.248**	0.039
SKUA-7A × SKUA-500	2.529**	-1.747	-2.056**	-1.840**	-1.786**	-27.379**	0.598**	-2.137**	-5.138**	2.903**	-0.054	-0.042
SKUA-11A × SKUA-500	2.951**	0.929	3.523**	0.204	1.062**	0.986	0.992**	0.572**	1.201**	0.324	-0.239**	0.009
SKUA-19A × SKUA-500	-1.892**	-4.887**	-1.320**	1.645**	0.265	12.146**	0.397	1.116**	2.917**	-2.445*	-0.063	0.044
SKUA-21A × SKUA-500	-3.588**	5.705**	-0.148	-0.009	0.460	14.248**	-1.987**	0.449**	1.020**	-0.782	0.357**	-0.011
SKUA-7A × Pusa Sugandh-3	2.779**	-2.809*	-1.061**	-1.452*	-0.661*	5.371**	-0.347	-0.302*	-0.321	-2.493*	0.204**	0.083*
SKUA-11A × Pusa Sugandh-3	-0.799*	-5.384**	0.262	-0.708	-0.913**	-11.864**	-2.773**	-0.927**	-2.015**	0.678	-0.014	0.000
SKUA-19A × Pusa Sugandh-3	1.691**	8.401**	2.375**	1.182	2.190**	16.396**	1.352**	1.361**	3.103**	-0.681	-0.138	-0.064

Table 4. Continued…

Cross combinations	Days to 50% flowering	Plant height	Flag leaf area	Number of tillers per plant	Panicle length	Number of spikelets per panicle	1000 Grain weight	Grain yield	Biological yield	Harvest index	Kernel length	Kernel breadth
SKUA-21A × Pusa Sugandh-3	-3.672**	-0.208	-1.576**	0.978	-0.615	-9.902**	1.768**	-0.133	-0.767**	2.496*	-0.052	-0.019
SKUA-7A × Pusa Basmati-1509	-5.971**	3.628**	0.014	-0.152	-0.036	19.096**	-0.382	1.166**	4.470**	-3.627**	-0.663**	0.041
SKUA-11A × Pusa Basmati-1509	8.118**	-6.896**	-3.623**	-5.508**	-2.688**	-36.039**	0.835**	-4.736**	-10.395**	-4.003**	-0.648**	0.025
SKUA-19A × Pusa Basmati-1509	-1.392**	1.638	1.417**	1.382*	1.715**	5.121**	-0.960**	1.198**	0.027	8.302**	0.262**	-0.039
SKUA-21A × Pusa Basmati-1509	-0.755*	1.630	2.192**	4.278**	1.010**	11.823**	0.506*	2.372**	5.898**	-0.672	1.048**	-0.027
CD95% SCA	0.700	2.276	0.676	1.191	0.638	3.341	0.417	0.249	0.339	2.097	0.142	0.071

**, ** = Significant at 0.05 and 0.01 levels, respectively*

SKUA-7A × RL-3 and SKUA-11A × RL-5 showed desirable heterosis as well as SCA effect for most of the traits *viz.,* grain yield, number of effective tillers per plant, panicle length and number of spikelets per panicle. The hybrid, SKUA-7A × RL-3 was top performer for grain yield, number of effective tillers per plant, panicle length and number of spikelets per panicle. Among female parents, SKUA-7A showed desirable GCA effect for most of the traits, while among male parents RL-1, RL-2, RL-11, SKUA-497, SKUA-494, SKUA-496 and SKUA-420 showed desirable GCA effect for maximum number of the traits.

The understanding of inheritance of various characters and the identification of superior parents are important pre-requisites for an efficient breeding programme. It is not always necessary that parents with high mean performance for yield and other traits would produce desirable F_1s or segregants [10]. Analysing and handling of a very large number of crosses resulting from numerous parents available would be a difficult and perhaps an impractical task. Therefore, selection of only few parents having high genetic potential in crossing programme is essential. In order to exploit the maximum heterosis using CMS system in the hybrid breeding programmes, we must know the combining ability effects of different male sterile and restorer lines for various traits [11,12]. Among the various techniques of combining ability analysis, line × tester analysis has been widely used for screening of germplasm to identify valuable donor parents and promising crosses [13,14,15].

4. CONCLUSION

In the present study, for most of the traits, SKUA-7A showed desirable GCA effect among the female parents; while RL-1, RL-2, RL-11, SKUA-497, SKUA-494, SKUA-496 and SKUA-420 showed desirable GCA effect amongst the male parents. Cross combinations SKUA-7A × RL-3 and SKUA-11A × RL-5 revealed desirable heterosis for most of the traits. These crosses also possessed desirable values of SCA effect for the traits. The combining ability evaluation has presumed great importance in plant breeding as it is a basic step for selection of potential parents for various hybridization programmes. Moreover, it provides an effective means for selecting specific crosses for further exploitation. The information provided regarding the nature of gene action would be helpful to determine an appropriate breeding strategy for the crop improvement.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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