

Combining Ability Analysis for Quality Traits in Selected Rice Varieties (*Oryza sativa* L.)

Nguyen Ba Thang

Independent researcher, Hoai Duc, Hanoi 13200, Vietnam

Abstract

Fifteen hybrid combinations developed by crossing five lines and three testers were assessed for milling and physio-chemical qualities to evaluate the combining ability of the parents using a line x tester design. This investigation provided information about the general combining ability (GCA) of parents and the specific combining ability (SCA) effects of crosses from eight popular inbred varieties. C70 was considered the best general combiner for the head rice recovery trait, while the crosses involving C70 with DH18 and CR203, 13/2 with TBR225 and Xi23, and OM6976 with TBR45 showed significant positive specific combining ability (SCA) effects. Xi23 and OM6976 among the lines showed significant general combining ability (GCA) effects indicating them to be good general combiners for obtaining hybrids with desirable (low or intermediate) properties of amylose content. The variances due to SCA were of greater magnitude than GCA for all the traits, revealing the preponderance of non-additive gene action for all the studied attributes. In all the studied quality traits, the narrow sense heritabilities were ordered as follows: head rice recovery > amylose content > gel consistency > alkali digestion > hulling percentage > milling percentage. The narrow sense heritabilities in these traits were quite low, ranging from 8.11% to 14.4%. Among the eight parents, C70, Xi23, and TBR225 were the most ideal for high-quality line breeding.

Keywords

Rice, combining ability, GCA, SCA, quality characters, line × tester.

Introduction

As a result of economic development and improvements in living standards, rice quality has become a major factor in rice production due to its effect on market value and farmer incomes (Clarete *et al.*, 2013). The primary components of rice grain quality influencing commercial value include appearance and milling, cooking, and eating

Received: March 4, 2024
Accepted: August 06, 2024

Correspondence to
nbthang@sina.com

ORCID
Nguyen Ba Thang
<https://orcid.org/0000-0001-8737-669X>

quality, which are determined by both physical and chemical properties. Of these, the head rice recovery determines rice producer incomes, whereas the amylose content of the rice grains is recognized as one of the most important determinants of eating and cooking quality. Success in any breeding program for improving traits such as grain quality depends upon the appropriate selection of parents and crosses. *Neobenedenia* spp. have a direct life cycle and short generation

Combining ability analysis is one of the useful tools available to determine the combining ability effects and helps breeders select desirable parents and hybrids for new variety development in many kinds of crops such as sorghum (Duan *et al.*, 2016), soybean (Otusanya *et al.*, 2022), corn (Yu *et al.*, 2020), sunflower (Jockovic *et al.*, 2018), common bean (Franco *et al.*, 2001), and rice (Asfaliza *et al.*, 2012; Maleki *et al.*, 2014). The line × tester analysis enables the estimate of different types of gene actions and also provides information about the general combining ability (GCA) of parents and the specific combining ability (SCA) effects of crosses (Kempthorne, 1957). The occurrence of non-additive gene effects for quality traits in rice has been found in earlier investigations for milling percentage, head rice recovery, amylose content, and gel consistency (Chen *et al.*, 2017; Buelah *et al.*, 2020; Bhatt *et al.*, 2022). Differences between broad-sense and narrow-sense heritability reveal the role of additive or non-additive gene effects in controlling rice quality traits and have been demonstrated by many scholars (Ao *et al.*, 2000; Deng *et al.*, 2006; Zhan *et al.*, 2015; Awad-Allah *et al.*, 2016). Therefore, the present investigation was undertaken to assess the combining ability of *indica* parents based on the performance of their hybrids, which will help breeders in identifying the parents and crosses that have desirable quality components.

Materials and methods

Plant materials and experimental design

Five high-yielding varieties (CR203, C70, 13/2, Xi23, and OM6976) were selected to cross

with three good quality varieties (DH18, TBR225, and TBR45) to produce 15 hybrids following the line × tester mating design (Kempthorne, 1957) in the 2021 summer season. The F₁s along with their parents were sown on the 25th January 2022 (spring season) in Hoai Duc district, Hanoi. The experiment was laid out in a randomized complete block design with three replications. Eighteen-day-old seedlings of the 15 F₁ hybrids along with their parents were transplanted in 3m-long rows per plot, at 1 seedling per hill and intra- and inter-row distances of 15cm and 20cm, respectively. Recommended field management practices were followed from transplanting to harvesting to raise a healthy crop.

After harvesting, 0.7-1.0kg of each genotype was sampled to measure milling quality (hulling quality, milling percentage, and head rice recovery) according to the procedures from the International Rice Research Institute (IRRI, 1996).

To test the hulling percentage (HULL), a known quantity of rough paddy was cleaned, air-dried to 13-14% moisture content, and dehulled with a McGill Laboratory Sheller. The hulling percentage was estimated as follows:

$$\text{Hulling percentage} = \frac{\text{Weight of hulled rice (g)}}{\text{Weight of rough rice (g)}} \times 100.$$

To estimate the milling percentage (MILL) after hulling, the brown rice was milled and polished in a Kett polisher for a standard time to get the milling percentage. The milling percentage was estimated as follows:

$$\text{Milling percentage} = \frac{\text{Weight of milled rice (g)}}{\text{Weight of rough rice (g)}} \times 100.$$

To test the head rice recovery percentage (HRR), the milled samples were screened to separate the whole grains from the broken ones. The small portion of broken kernels that passed along with the whole kernels were separated by hand. Head rice recovery, which is the estimate of full size plus three-fourth size kernels, was expressed in the following percentage:

$$\text{Head rice recovery} = \frac{\text{Weight of head rice (g)}}{\text{Weight of rough rice (g)}} \times 100.$$

The amylose content was measured by the procedures described by TCVN5716: 2008, gel

consistency was estimated according to TCVN8369: 2010, and alkali digestion was determined following the protocol of TCVN 5715: 1993. For alkali digestion, a seven-point scale was used in assigning different values based on kernel spreading (IRRI, 1996).

Data analysis

Statistical analysis was carried out using sample mean values. The data were analyzed for combining ability according to Griffing's (1956) model I (genotypes and blocks as fixed-effects) and their variance was calculated using the "Agricolae" package in Rstudio version 4.0.5 and Excel according to the model suggested by Kempthorne (1957).

Results and discussion

Variance and combining ability variance analysis

The analysis of variance revealed significant differences among genotypes including the lines, testers, and crosses (**Table 1**) in most of the characteristics. This implied that the treatments had wide genetic diversity among themselves. The GCA variance of the lines was found to be significant or highly significant for almost all the investigated quality traits, except for the milling percentage trait, which confirmed that the lines in this study did not influence the milling percentage but had different effects on other trait expressions in the crosses. Analysis of the tester GCA variance showed non-significant effects on the hulling percentage and gel consistency traits but highly affected the milling percentage, head rice recovery, amylose content, and alkali digestion traits, which implied that the testers had different influences on the studied trait expressions in different crosses.

The major role of the non-additive gene effects in the performance of all the traits was determined by a lower value of the general combining ability variance (δ_{gca}^2) than the specific combining ability variance (δ_{sca}^2). In this study, the ratio of $\delta_{gca}^2 / \delta_{sca}^2$ was less than unity for all the quality traits, indicating a preponderance of non-additive genetic variance

(**Table 1**). This suggested a greater role of non-additive gene action in their expression and offers good prospects of the exploitation of genetic variation for grain and its component characteristics through hybrid breeding.

Analysis of combining ability effects

* Significant at the 0.05 level and ** Significant at the 0.01 level

The GCA effects manifested significant differences. The GCA effects of the same traits or of the same male or female parent were varied, indicating there was no consistent trend for the genotypes or quality traits (**Table 2**). Regarding the milling quality traits, head rice recovery is rice's most important quality parameter since it is positively related to the grower's preference and income in most rice segments. The C70 variety was identified as having the highest GCA effect (4.04) followed by 13/2 (2.87), and OM6976 had the lowest negative effect (-7.21), whereas only DH18 expressed a significantly positive GCA effect, and TBR45 and TBR225 were determined to have significantly negative GCA effects in the tester group for head rice recovery. This implied that C70 and DH80 exhibited good general combining ability effects for this trait.

For the physio-chemical traits like gel consistency, amylose content, and alkali digestion, the choice of parents for developing specific crosses depends on consumer preference. Current customers expect low amylose content, high gel consistency, and medium alkali digestion. Among the lines, Xi23 and OM6976 showed significantly negative GCA effects for the amylose content traits whereas CR203 and 13/2 exhibited significant positive ones. For the testers, TBR45 and TBR225 displayed significantly negative effects whereas DH18 was found to have a significantly positive effect for the amylose content trait. Regarding the gel consistency, all the lines showed highly significant effects ($P < 0.01$), and only OM6976 among the lines was found to have a positive GCA effect, whereas no tester had a GCA effect for the gel consistency trait (**Table 2**).

Table 1. Analysis of variance for combining ability for the six investigated quality traits

Variance source	DF	HUL	MIL	HRR	AC	GC	ALK
Replication	2	0	0.07	1.2	0.02	1.06	0.19
Genotypes	22	3.97**	10.82**	80.71**	29.90**	677.36**	5.71**
Parents	7	6.31**	14.00**	50.44**	68.38**	1249.69**	6.85**
Parents vs crosses	1	17.49**	11.55**	234.59**	56.39**	5975.5**	0.24
Crosses	14	1.83**	9.18**	84.85**	7.52**	14.76**	5.52**
Line	4	4.05*	9.76	173.08**	15.47**	46.09**	9.06*
Tester	2	1.49	24.77*	190.82**	15.82**	0.62	14.46**
Line x Tester	8	0.80**	4.99**	14.25**	1.48**	2.62**	1.52**
Error	44	0.04	0.21	0.73	0.01	0.75	0.25
$\bar{\sigma}_{gca}^2$		0.04	0.15	2.50	0.21	0.43	0.14
$\bar{\sigma}_{sca}^2$		0.26	1.59	4.51	0.49	0.62	0.42
$\bar{\sigma}_{gca}^2 / \bar{\sigma}_{sca}^2$		0.14	0.09	0.55	0.44	0.69	0.34

Note: HUL: hulling percentage (%), MIL: milling percentage (%), HRR: head rice recovery (%), AC: amylose content (%), GC: gel consistency (mm), ALK: alkali digestion (score)

* Significant at the 0.05 level and ** Significant at the 0.01 level

Table 2. Effects of general combining ability for the main quality characteristics in the parents

Parents	HUL	MIL	HRR	AC	GC	ALK
Lines						
CR203	-0.72 **	-1.44 **	-0.24	1.03 **	-1.6 **	-1.09 **
C70	0.2	1.22 *	4.04 **	0.04	-2.04 **	1.13 **
13/2	0.82 **	0.77 *	2.87 **	1.54 **	-1.16 **	-0.98 **
Xi23	0.36 **	-0.13	0.54	-1.22 **	1.73 **	1.02 **
OM6976	-0.66 **	-0.42	-7.21 **	-1.4 **	3.07 **	-0.09
Testers						
DH18	-0.26 **	0.62 **	3.99 **	1.05 **	-0.04	-0.73 **
TBR45	-0.08	-1.48 **	-1.12 **	-1.02 **	0.22	-0.13
TBR225	0.35 **	0.86 **	-2.88 **	-0.03 **	-0.18	0.87 **
SE (gi for line)	0.063	0.151	0.285	0.063	0.29	0.127
SE (gj for tester)	0.049	0.117	0.221	0.049	0.224	0.098
SE (gi-gj) line	0.089	0.214	0.403	0.089	0.41	0.179
SE (gi-gj) tester	0.069	0.166	0.312	0.069	0.317	0.139

Note: HUL: hulling percentage (%), MIL: milling percentage (%), HRR: head rice recovery (%), AC: amylose content (%), GC: gel consistency (mm), ALK: alkali digestion (score)

Table 3. Effects of specific combining ability for the main quality characteristics in the F₁ combinations

Cross	HUL	MIL	HRR	AC	GC	ALK
CR203 × DH18	0.43 **	1.3 **	0.78	-0.02	0.27	0.87
CR203 × TBR45	0.12	-2.27 **	-2.82 **	-0.28 **	0.67 **	0.20
CR203 × TBR225	-0.55 **	0.97 **	2.04 **	0.29 **	-0.93 **	-1.07
C70 × DH18	0.18	-0.62 *	0.03	0.25 **	-0.62 **	-0.13
C70 × TBR45	-0.14	0.71 *	0.24	-0.03	-0.89 **	-0.47
C70 × TBR225	-0.04	-0.09	-0.27	-0.26 **	1.51 **	0.60
13/2 × DH18	-0.85 ***	-1.28 **	-1.09 *	0.78 **	0.49 *	0.20
13/2 × TBR45	0.47 **	1.36 **	-1.08 *	-0.13	0.22	0.20
13/2 × TBR225	0.38 **	-0.78 **	2.18 **	-0.66 **	-0.71 **	-0.40
Xi23 × DH18	0.28 *	0.16	0.50	-1.25 **	-0.40 *	0.36
Xi23 × TBR45	-0.04	-0.21	2.54 **	0.77 **	0.67 **	0.36
Xi23 × TBR225	-0.24 *	0.6 *	-3.04 **	0.48 **	-0.27	0.71
OM6976 × DH18	-0.04	0.44	-0.21	0.22	0.27	-0.58
OM6976 × TBR45	-0.42 **	0.41	1.13 *	-0.36 *	-0.67 **	0.42
OM6976 × TBR225	0.45 **	-0.86 **	-0.91	0.14	0.4 *	0.16
SE (gij-sca effect)	0.11	0.26	0.49	0.07	0.50	0.29
SE (gsij-skl)-tester	0.15	0.37	0.70	0.10	0.71	0.41

Note: HUL: hulling percentage (%), MIL: milling percentage (%), HRR: head rice recovery (%), AC: amylose content (%), GC: gel consistency (mm), ALK: alkali digestion (score)

* Significant at the 0.05 level and ** Significant at the 0.01 level

The SCA values in **Table 3** show a complex SCA effect variance. In the same quality trait or the same combination, the SCA effects displayed significantly different values manifesting diversification of gene interactions. Huge differences were observed in the SCA values within the same trait due to different crosses and in the same cross, the SCA effects for different quality traits were comparatively different. The cross involving 13/2 × TBR225 showed significant positive SCA effects (2.18), since it was a high × low GCA parental cross, whereas the crosses of CR203 × TBR225 and Xi23 × TBR45 showed significant positive SCA effects (2.04 and 2.54, respectively), as they involved parents with average × average GCA effects for the head rice recovery trait. However, only one cross, viz. OM6976 × TBR45, had a significantly positive SCA effect (1.13), as it involved low × low parents for the same trait. Amylose content is an important physio-chemical determinant of cooking and eating quality. Among the five combinations that displayed desirable GCA effects with high significance levels, namely CR203 × TBR45 (-0.28), C70 × TBR225 (-0.26), 13/2 × TBR225 (-0.66), Xi23 × DH18 (-1.25), and OM6976 × TBR45 (-0.36), three crosses were made from high × low parents, one cross from average × low parents, and one cross from low × low GCA parents. Regarding the gel consistency, among the fifteen *indica/indica* crosses, no combination displayed significantly negative SCA effects whereas the cross of C70 × TBR225 showed highly positive SCA effects (1.51) ($P < 0.01$). Overall, no excellent combination for all the studied traits was found, but 13/2 × TBR225 and OM6976 × TBR45 were excellent combinations for both the head rice recovery and amylose content traits.

The reflection of the SCA effect in the superior specific combinations (**Table 3**) towards the desirable direction for the different quality characters highlighted that these superior crosses involved all the possible combinations between parents, namely (high × high), (high × average), (high × low), (average × average), (average × low), and (low × low) GCA effects.

Analysis of combining ability variance and heritability components

The GCA effect variance, SCA effect variance, the proportion of genotypic variance (V_g , V_s), contribution, broad sense heritability, and narrow sense heritability for each quality trait are presented in **Table 4**.

The ratio of the GCA effect variance to the SCA effect variance of all the quality traits, viz. hulling percentage, milling percentage, head rice recovery, amylose content, gel consistency, and alkali digestion traits, was lower than unity (< 1), revealing that non-additive gene action played a very important role in all the investigated traits in the hybrids.

Franco *et al.* (2001) stated that the SCA effects of hybrids alone had limited power in a breeding program. As such, the SCA effect must be used in combination with other parameters such as hybrid means (high performance *per se* hybrid) and the GCA of the respective parents. The GCA effects of the line and tester parents in the different quality traits were different, indicating no consistent relationship between the GCA effects from the lines and testers in this study. The variance of the GCA effects of the tester in the milling percentage was higher than that of the line, implying that the contribution of the GCA effect in this trait from the male line was higher than the female line. In contrast, the variances of the GCA effects of the lines in the hulling percentage, head rice recovery, amylose content, gel consistency, and alkali digestion were much higher than that of the testers, showing that the female genotypic variance contributed much more than the male genotypic variance for these traits.

The heritability value gives an overview of the non-additive type of genetic influence on plant appearance (Yunus & Paroda, 1982; Schmidt *et al.*, 2019), whereas the information on the correlation between characteristics makes it easier to choose the desired plant characteristics (Amzeri *et al.*, 2021). From **Table 4**, the descending order of broad sense heritabilities was amylose content, head rice recovery, hulling percentage, milling percentage, alkali digestion,

Table 4. Estimates of the variance components of combining ability, proportional contribution, and heritability for the six quality traits

Trait	Genotypic variance							Broad-sense heritability (%)	Narrow-sense heritability (%)
	δ_1^2	δ_2^2	δ_{12}^2	V_g (%)	V_{g1} (%)	V_{g2} (%)	V_s (%)		
Hulling percentage (HULL)	0.36	0.05	0.26	74.90	63.27	11.63	25.09	94.86	10.39
Milling percentage (MIL)	0.53	1.32	1.59	68.92	30.37	38.55	31.07	94.35	8.11
Head rice recovery (HRR)	17.65	11.77	4.50	90.40	58.28	32.12	9.59	97.89	14.40
Amylose content (AC)	1.56	0.96	0.49	88.79	58.76	30.03	11.21	99.54	14.20
Gel consistency (GC)	4.83	0	0.62	89.84	89.24	0.60	10.15	87.57	14.12
Alkali digestion (ALK)	0.94	0.52	0.69	76.13	51.89	24.23	23.87	93.34	11.32

Note: δ_1^2 , δ_2^2 , and δ_{12}^2 represent lines, testers, and cross variance, respectively

V_g (%), V_{g1} (%), V_{g2} (%), and V_s (%) express proportional contributions of general combining ability, line, tester, and cross variance to the total variance, respectively.

and gel consistency (ranging from 99.54 to 87.57%). Among them, the broad sense heritabilities of the head rice recovery and amylose content were higher than 95%, while the hulling percentage, milling percentage, and alkali digestion were higher than 90%, and the lowest was gel consistency (87.57). The narrow sense heritabilities of the six studied quality traits were quite low, ranging from 8.11 to 14.4%, although the highest specific heritability was calculated for head rice recovery (14.40%). The descending order of narrow sense heritabilities was head rice recovery, amylose content, gel consistency, alkali digestion, hulling percentage, and milling percentage. The narrow-sense heritability values of most of the traits were not consistent with the trends of the broad-sense heritability values, however, the difference between the broad-sense and narrow-sense heritability values was very high, revealing that additive gene effects played an important role in controlling these quality traits. Similar findings have also been demonstrated by many scholars (Ao *et al.*, 2000; Zhang *et al.*, 2003; Deng *et al.*, 2006; Zhan *et al.*, 2015; Awad-Allah *et al.*, 2016; Chen *et al.*, 2017).

Conclusions

Parental genotypes and their hybrid combinations displayed significant variation, indicating substantial genetic variability that could be useful for further breeding programs. The computed ratio of the GCA/SCA variations showed the dominance of non-additive gene action governing inheritance for all six quality traits. For the most important quality characteristics, such as head rice recovery, C70, 13/2, and DH18 were identified as good combiners whereas Xi23, OM6976, TBR45, and TBR225 were desirable combiners for the amylose content trait. Among the crosses, 13/2 × TBR225, Xi23 × DH18, and OM6976 × TBR45 were determined to be the best combinations for the exploitation of almost all the quality traits since they displayed highly significant SCA effects at the 1% probability level. The studied quality traits were mainly influenced by the male genotype, except for the milling percentage.

Narrow sense heritability in the studied traits was quite low and the highest heritability was for head rice recovery. The results derived from this study would be highly useful in rice breeding programs and may be used for further crop improvement by selecting early recombinants of milling and physio-chemical quality attributes.

References

- Amzeri A., Badami K., Gita P., Alfiyan Syah M. & Setiadi Daryono B. (2021). Phenotypic and genetic diversity of watermelon (*Citrullus lanatus*) in East Java, Indonesia. *Biodiversitas Journal of Biological Diversity*. 22(11): 5223-5230.
- Ao Y., Xu, C. W. & Mo H. D. (2000). Quantitative analysis for inheritance of quality characters in *indica* hybrid rice. *Acta Genetica Sinica*. 27(8): 706-712 (*in Chinese*).
- Asfaliza R., Rafii M., Saleh G., Omar O. & Puteh A. (2012). Combining ability and heritability of selected rice varieties for grain yield. *Australian Journal of Crop Science*. 6(12):1718-1723.
- Awad-Allah M. M. A., Wissa M. T. & Elmoghazy A. M. (2016). Line x tester analysis and heterosis for grain quality characters of some parental lines of hybrid rice (*Oryza sativa* L.). *Minufiya Journal of Agricultural Research*. 41(3): 567-686.
- Bhatt N., Nautiyal M. K., Vikasmangal & Bhatt L. (2022). Combining ability analysis for grain quality characters of diverse CMS lines in hybrid rice. *Biological Forum - An International Journal*. 14(1): 73-77.
- Buelah J., Ram Reddy V. & Balaram N. (2020). Studies on combining ability and gene action for yield and quality traits in hybrid rice (*Oryza sativa* L.). *International Journal of Current Microbiology and Applied Sciences*. 9(12): 1282-1290.
- Chen X. C., Bai Y. S., Wang S. M., Mei D. Y., Gong C. L., Han Y. F., Yu Z. K., Du S. Y. & Zhu L. N. (2017). Combining ability and heritability of grain quality of upland japonica hybrid rice. *Chinese Agricultural Science Bulletin*. 33(22): 1-6.
- Clarete R. L., Adriano L. & Esteban A. (2013). Rice trade and price volatility: Implications on ASEAN and global food security. *Asian Development Bank Economics Working Paper Series* (Asian Development Bank, Metro Manila, Philippines, 2013).
- Deng H. F., He Q., Mao Y. C., Xu Q. G., Shu F., Zhang W. H., Yang F. & Yuan L. P. (2006). Quantity characters and their combining ability of early hybrid rice in Yangtze rice area. *Acta Agonomica Sinica*. 32(5): 633-639 (*in Chinese*).
- Duan B., Liu Q. S., Liang D., Yan F. X. & Guo Q. (2016). Analysis on the combining ability of quality traits in forage sorghum. *Crops*. 32(1): 51-55 (*in Chinese*).

- Falconer D. S. & Mackay T. F. C. (1996). Introduction to Quantitative Genetics, fourth ed. Pearson Education Limited, England, United Kingdom.
- Franco M., Cassini S., Oliveira V., Vieira C., Tsai S. M. & Cruz C. D. (2001). Combining ability for nodulation in common bean (*Phaseolus vulgaris* L.) genotypes from Andean and middle American gene pools. *Euphytica*. 118(3): 265-270. DOI: 10.1023/a:10175 60118666.
- Griffing B. (1956). Concept of general and specific combining ability in relation to diallel crossing system. *Australian Journal of Biological Sciences*. 9: 463-493. DOI: 10.1071/BI9560463.
- IRRI (1996). Standard evaluation system for rice. 4th Edition, IRRI, The Philippines.
- Jockovic M., Jovic S., Prodanovic S., Cvejic S., Ciric M., Canak P. & Marjanovic Jeromela A. (2018). Evaluation of combining ability and genetic components in sunflower. *Genetika*. 50(1): 187-198. DOI: 10.2298/GENSR1801187J.
- Kempthorne O. (1957). An introduction of genetics statistics. John Wiley and Sons, New York, USA. 458-471.
- Maleki M., Fotokian M. H., Kajouri F. D., Nouri M. Z. & Agahi K. (2014). Study of combining ability and gene action of cooking quality traits in rice (*Oryza sativa* L.) using line \times tester analysis. *Journal of Biodiversity and Environmental Sciences*. 4(3): 220-226.
- Otusanya O. G., Chigeza G., Chander S., Abebe A. T., Sobowale O. O., Ojo D. K. & Akoroda M. O. (2022). Combining ability of selected soybean parental lines. *Indian Journal of Agricultural Research*. 56: 7-1. DOI: 10.18805/IJARE.A-638.
- Schmidt P., Hartung J., Bennewitz J. & Piepho, H. P. (2019). Heritability in plant breeding on a genotype-difference basis. *Genetics*. 212(4): 991-1008.
- Yu K., Wang H., Liu X., Xu C., Li Z., Xu X., Liu J., Wang Z. & Xu Y. (2020). Large-scale analysis of combining ability and heterosis for development of hybrid maize breeding strategies using diverse germplasm resources. *Front Plant in Science*. 11, 660. DOI: 10.3389/fpls.2020.00660.
- Yunus M. & Paroda R. S. (1982). Impact of biparental mating on correlation coefficients in bread wheat. *Theoretical Applied Genetics*. 62(4): 337-343. DOI: 10.1007/BF00275098.
- Zhan X. C., Zheng L. Y., Zou Y., Qian B. Y., Zhang P. J. & Dong Z. R. (2015). Analysis of heterosis, combining ability and heritability of quality characters in Japonica hybrid rice. *Journal of Anhui Agricultural University*. 42(6): 968-973 (*in Chinese*).
- Zhang L. H., Wang L. Y. & Wang J. J. (2003). Studies on combining ability and heritability of milling and physical properties in indica hybrid rice. *Acta Agriculturae Nucleatae Sinica*. 17(6): 417-422 (*in Chinese*).