Heterosis and Combining Ability Analysis for Yield and Related-Yield Traits in Hybrid Rice

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Abstract

Study of combining ability and heterosis were conducted on 12 F_1 hybrids along with seven rice genotypes (three cytoplasmic male sterile lines and four restorer varieties) to know the pattern of inheritance of some morphological traits for selecting superior genotypes. The experiment was carried out according to line x tester mating design, during 2007-08. Analysis of variance revealed significant differences among genotypes, crosses, lines, testers and line x tester interactions for tiller number, plant height, days to 50% flowering, panicle length, number of spikelets per panicle, spikelet fertility and grain yield traits. Variances of SCA were higher than the GCA variances for traits except for plant height which indicated predominance of non-additive gene action in the inheritance of the traits. The highest heterosis (106.60%) was observed in cross IR68899A x Poya followed by other eight crosses for yield and most of its related traits. The proportional contribution of testers was observed to be higher than that of the interactions of line x tester that revealed the higher estimates of GCA variance that is additive gene action among the testers used. Within CMS parents, IR62829A and among male parents, IR50 and Poya were observed to be good general combiners for most of the characters studied. The cross combinations IR62829A x Mosa-tarom, IR68899A x Poya, IR58025A x IR50 and IR58025A x Poya were observed to be good specific cross combinations for grain yield and most of its related traits due to highly significant SCA and heterotic effects.

Keywords: Heterosis, Combining ability and Hybrid Rice

1. Introduction

Breeding strategies based on selection of hybrids require expected level of heterosis as well as the specific combining ability (SCA). In breeding high yielding varieties of crop plant, the breeders often face with the problem of selecting parents and crosses. Combining ability analysis is one of the powerful tools available to estimate the combining ability effects and aids in selecting the desirable parents and crosses for the exploitation of heterosis (Sarker et al., 2002; Rashid et al., 2007). Presence of heterosis and SCA effects for yield and its related traits are reported by Nuruzzaman et al., 2002; faiz et al., 2006 and saleem et al., 2008. To exploit maximum heterosis using cytoplasmic male sterile (CMS) technique in the hybrid programme, we must know the combining ability of different male sterile and restorer lines.

The performance of parent may not necessarily reveal it to be a good or poor combiner. Therefore, gathering information on nature of gene effects and their expression in terms of combining ability is necessary. At the same time, it also elucidates the nature of gene action involved in the inheritance of characters. General combining ability (GCA) is attributed to additive gene effects and additive x additive epistasis and is theoretically fixable. On the other hand, specific combining ability attributable to non-additive gene action may be due to dominance or epistasis or both and is non-fixable. The presence of non-additive genetic variance is the primary justification for initiating the hybrid programme (Cockerham, 1961; Pradhan et al., 2006). There is need to study various morphological traits to get better understanding of inheritance and select or identify superior genotypes. Heritability values have been variable depending upon the genetic nature of genotypes for different morphological characters (Vivek et al., 2000; Mishra and Verma, 2002; Mahto et al., 2003; Swati and Ramesh, 2004). Heterosis estimates were attributed to both additive and high degree of dominance or epistasic interactions or both for one or more morphological traits. Vanaja and Babu (2004) pointed out that yield increase in rice was due to favorable heterosis in flag leaf area, number of spikelets per panicle and number of grains per panicle.

In this paper an attempt has been made to assess the combining ability and to determine the nature and magnitude of gene action for yield and yield-related traits to explore the best combination of made sterile and restorer lines for the exploitation of maximum heterosis or hybrid vigor in F_1 hybrids for tiller number, plant height, days to 50% flowering, panicle length, number of spikelets per panicle, spikelet fertility and grain yield traits.

2. Materials and Methods

2.1 Plant materials

The experimental materials comprised seven rice genotypes, three genotypes (IR58025A, IR62829A and IR68899A) were used as females (designated as lines) and four genotypes (Amol-2, IR50, Poya and Mosa-tarom) designated as testers were used as males. These parents were crossed to produce 12 F_1 hybrids according to line x tester mating design (Kempthorne, 1957). This study was conducted in 2007 – 2008 years at Research Field of Sari Agricultural Sciences and Natural Resources University. Single seedlings of each entry were transplanted at 20 x 20 cm spacing in 3 x 5 m^2 plots in a randomized complete block design with three replications. In this study seven traits includes tiller number per hill, plant height (cm), days to 50% flowering, panicle length (cm), number of spikelets per panicle, spikelet fertility percentage and grain yield per 10 plants (gr) were evaluated based on standard evaluation system rice (Scshu, 1988).

2.2 Statistical analysis

Data were recorded on ten randomly selected plants from parents and F_1s plant samples. Heterosis was estimated from mean values according to Fehr (1987) and t-test was performed. Combining ability analysis was done using line x tester method (Kempthorne, 1957). The variances for general combining ability and specific combining ability were tested against their respective error variances derived from ANOVA reduced to mean level. Significance test for GCA and SCA effects were performed using t-test. Midparent heterosis (Ht) and high-parent heterosis (Htb) or heterobeltiosis were determined as outlined by Falconar and Mackay (1996).

3. Results

3.1 Means of the estimated traits

Mean of lines, testers and their hybrids (Table 1) indicated worth of genetic variability for the improvement of tiller number per hill, plant height (cm), days to 50% flowering, panicle length (cm), number of spikelets per panicle, spikelet fertility (%) and grain yield traits, which are important in hybrid rice yield. Mean of traits classified using Duncan's multiple range test (p = 0.05). Line of IR58025A produced the highest panicle length, number of spikelets per panicle and grain yield. Plant height and days to 50% flowering were least in IR68899A and IR62829A lines, respectively. Also Amol-2 tester produced the highest tiller number and spikelets fertility, IR50 variety produced the highest number of spikelets per panicle and grain yield. The longest panicle length was given by Moosa-tarom, but plant height and days to 50% flowering traits were least in IR50 and Poya varieties, respectively. Significant differences among various traits have been observed earlier reports (Surek and Korkut, 2002; Swati and Ramesh, 2004). There results showed that different genetic systems involved in controlling traits, which emphasized on important of study of these traits.

Analysis of variance of combining ability revealed significant differences among genotypes, crosses, lines, testers and line x tester interactions. The significant differences among the lines, testers and lines x testers indicated that the genotypes had wide genetic diversity among themselves for all traits (Table 2). The significance of the means of sum of squares due to lines and testers indicated a prevalence of additive variance. However, significant differences due to interactions of line x tester for all the characters, indicating the importance of both additive and non-additive variance. Variances of SCA were higher than the GCA variances for these characters except for plant height which indicated preponderance of non-additive gene action in the inheritance of the traits. This was further supported by low magnitude of MSgca/MSsca ratios (Table 2). It suggested greater importance of non-additive gene action in its expression and indicated very good prospect for the exploitation of non-additive genetic variation for traits through hybrid breeding (Ramalingam, 1997; Annadurai and Nadarajan, 2001).

The proportional contribution of lines, testers and their interactions to total variances showed that testers played an important role toward for traits, indicating predominant testers influence for these traits (Table 3). The smaller contribution of interactions of the line x tester than testers, indicating higher estimates of variances due to general combining ability. Rissi et al. (1991) observed higher estimates of GCA variances due to testers in rice. Contribution of interactions of line x tester was higher than lines for tiller number, number of spikelets per panicle, spikelet fertility and grain yield, indicating higher estimates of GCA variances for interaction. For example grain yield in IR58025A x Poya cross was 571.37 (gr), but in IR62829A x Poya and IR68899A x Poya crosses were 628.30 (gr) and 809.93 (gr), respectively.

3.2 Combining ability analysis

There were significant differences among the genotypes for characters (Table 2), which lead to the combining ability analysis. Thus were partitioned genetic effects between genotypes into General Combining Ability and Specific Combining Ability. Regarding to the significance of g_i in two directions in traits, we can declare that parents have potential of transfer of high and low values for each trait. Hence, in cases which increasing and decreasing the value of traits are desired, we should consider positive and negative values of g_i, respectively. Therefore, for plant height and days to 50% flowering negative GCA and SCA effects were desirable, while in case of other characters positive GCA and SCA effects were desirable.

3.2.1 General combining ability

None of the CMS lines or pollinators was found to be good general combiner for all the characters studied. Female parents, IR68899A and IR62829A were observed as a good general combiner due to its highly significant and positive GCA effects for grain yield and desirable GCA effects for days to 50% flowering (Table 4). Singh et al. (1996) and Watanesk (1993) in rice observed good CMS parents for yield and its contributing traits. The pollinator, Poya was the best general combiner due to highly significant GCA effects for grain yield and most of the yield contributing traits. IR50 showed highly significant GCA effects for grain yield with all other desirable GCA effects, except panicle length. It was considered to be a good general combiner pollinator followed by Amol-2 variety (Table 4). Rogbell *et al*. (1998) and Singh *et al*. (1996) observed similar good general combiner male parents for yield in rice. Desirable GCA effects were observed in 2 parents (IR50 and Poya) for tiller number, 3 parents (IR62829A, Amol-2 and IR50) for reduced plant height, 4 parents (IR68899A, Amol-2, IR50 and Poya) for reduced days to 50% flowering, 2 parents (IR58025A and Mosa-tarom) for panicle length, 1 parent (IR50) for number of spikelets per panicle, 4 parents (IR62829A, Amol-2, IR50 and Poya) for spikelet fertility (%) and 5 parents (IR62829A, IR68899A, Amol-2, IR50 and Poya) for grain yield (Table 4). Above parents were considered to be good general combiners for these characters, respectively.

3.2.2 Specific combining ability

The cross combination IR62829A x Mosa-tarom was the best specific cross combination for the highest and significant SCA effects for grain yield with desirable character for spikelet fertility (%). The cross IR68899A x Poya showed significant or non-significant desirable SCA effects for yield and 5 yield related traits. The cross IR58025A x IR50 for most of the characters except plant height, panicle length and number of spikelets per panicle, cross IR58025A x Poya for grain yield, the cross IR68899A x Amol-2 for all characters and the cross IR58025A x Amol-2 for grain yield and days to 50% flowering showed significant desirable SCA effects (Table 5). Above cross combinations were found to be good specific combinations with high heterotic effects for grain yield along with most of the yield contributing characters. Singh et al. (1996) and Rogbell et al. (1998) found good specific cross combinations in rice. None of the cross combinations were found to be good specific cross combinations for all the characters studied (Table 5). Generally, in most of the good specific cross combinations at least one low general combiner parents were involved for all the characters along with grain yield. It also indicated both additive and non-additive types of gene action. Two crosses high x high general combiners (IR68899A x Amol-2 and IR68899A x Poya) were involved for production of good specific cross combinations in many characters in which additive type of gene action was found.

3.3 Evaluation of heterosis

The data on estimates of heterosis (Ht) and heterobeltiosis (Htb) revealed that midparent heterosis for tiller number ranged -19.5 to 92.4 percent and that of high-parent heterosis was -22.6 to 80.34 percent (Table 6). Nine hybrids indicated significantly positive heterosis as well as heterobeltiosis. Out of these six hybrids viz. IR58025A x IR50 (Ht = 92.24, Htb = 80.34), IR58025A x Poya (Ht = 67.60, Htb = 37.17), IR62829A x IR50 (Ht = 66.79, Htb = 62.43), IR62829A x Poya (Ht = 88.24, Htb = 43.81), IR68899A x IR50 (Ht = 15.88, Htb = 13.98) and IR68899A x Poya (Ht = 77.10, Htb = 36.26) were important based on higher mean performance and highly significant heterosis of both types. Over-dominant type of gene action was suggested for them. Three hybrids (IR62829A x Amol-2, IR68899A x Amol-2 and IR68899A x Mosa-tarm) showed significant and positive mid-parent heterosis but non-significant positive heterobeltiosis manifesting partial dominant type of gene action, while IR62829A x Mosa-tarom indicated non-significant heterosis and heterobeltiosis displaying additive type of gene action. These results are in agreement with earlier findings (Vanaja and Babu, 2004; Verma et al., 2002).

Negative heterosis for plant height is desirable for breeding short statured hybrids and varieties. None of the hybrids manifested significantly negative mid-parent and high-parent heterosis for plant height. The extent of heterosis over mid-parent was -0.14 to 18.75 percent and that of better parent was -32.20 to 3.41 percent. Six hybrids indicated intermediate plant height (101.66 to 126.5 cm) out of which one hybrid viz. IR58025A x IR50 (Ht = 18.75, Htb = 3.41) had significant positive midparent and high-parent heterosis and four hybrids IR58025A x Mosa-tarom (Ht = -0.14, Htb = -30.2), IR62829A x IR50 (Ht = 2.02, Htb = -16.60), IR62829A x Poya (Ht = 0.32, Htb = -27.7) and IR62829A x Mosa-tarom (Ht = 1.05, Htb = -32.20) had non-significant heterosis and negative significant heterobeltiosis. Among theses, two hybrids (IR58025A x IR50 and IR62829A x Poya) were high yielding. Other two highest yielding hybrids were of intermediate stature and positive significant mid-parent heterosis and negative significant high parent heterosis viz IR68899A x Poya (Ht = 4.76, Htb = -23.9) and IR68899A x Amol-2 (Ht = 10.38, Htb = -9.33).

Negative heterosis for days to 50% flowering is desirable for breeding short statured hybrids and varieties. Ten of the hybrids manifested significantly negative mid-parent and high-parent heterosis for days to 50% flowering. Six hybrids indicated short days to 50% flowering (53.0 to 61.33 days), which all hybrids had negative significant mid parent and high-parent heterosis. Out of which there hybrids viz IR62829A x Poya, IR68899A x Amol-2 and IR68899A x Poya were high yielding.

For panicle length, five hybrids viz IR58025A x Amol-2 (28.17 cm), IR58025A x IR50 (31.33 cm), IR58025A x Mosa-tarom (41.33 cm), IR62829A x Amol-2 (25.9 cm) and IR68899A x Amol-2 (26.53 cm) were important based on highly significant heterosis of both types. Over-dominant type of gene action was suggested for them. Three hybrids (IR58025A x Poya, IR68899A x IR50 and IR68899A x Poya) showed significant and positive mid-parent heterosis but non-significant heterobeltiosis manifesting partial dominant type of gene action.

For spikelets per panicle, eight hybrids namely IR58025A x Poya (Ht = 21.32, Htb = 20.39), IR58025A x Mosa-tarom (Ht = 50.37, Htb = 27.71), IR62829A x Amol-2 (Ht = 38.57, Htb = 37.61), IR62829A x IR50 (Ht = 43.84, Htb = 12.02), IR62829A x Poya (Ht = 45.94, Htb = 17.72), IR62829A x Mosa-tarom (Ht = 33.40, Htb = 26.18), IR68899A x Amol-2 (Ht = 42.44, Htb = 28.60) and IR68899A x Mosa-tarom (Ht = 56.27, Htb = 48.74) had significantly positive heterosis and heterobeltiosis manifesting over dominance type of gene action. Four hybrids viz. IR58025A x Amol-2 (Ht = 23.71, Htb = -0.14), IR58025A x IR50 (Ht = 11.73, Htb = 5.88), IR68899A x IR50 (Ht = 27.26, Htb = 7.67) and IR68899A x Poya (Ht = 13.23, Htb = -0.28) had significantly positive heterosis but significant or non-significant negative heterobeltiosis indicating partial dominance type of gene action for increased number of spikelets per panicle. All these 13 hybrids can be regarded as promising based on higher mean performance and both types of heterosis for the improvement of number of spikelets per panicle.

For spikelet fertility, minimum mid-parent heterosis (-56.90 %) was expressed by cross IR58025A x Mosa-tarom with 19.75 % spikelet fertility and maximum (134.40) by IR58025A x IR50 with 86.79% spikelet fertility. Similarly, minimum high-parent heterosis (-78.30) was shown by IR68899A x Mosa-tarom and maximum (17.18) by IR58025A x IR50. Based on higher mean performance and desirable heterosis and heterobeltiosis, five hybrids (IR58025A x IR50, IR62829A x Amol-2, IR62829A x Poya, IR68899A x Amol-2 and IR68899A x Poya) were found to be the potential hybrids for higher panicle fertility. Also these five hybrids were high yielding.

For grain yield, heterosis and heterobeltiosis was -78.4 to 147.20 and -81.30 to 106.60, respectively. Nine hybrids manifested significantly positive heterosis and heterobeltiosis. Over dominant type of gene action was suggested for most of them. Similar results were obtained by Gnansekaran et al. (2006). The predominant role of dominant type of gene action was attributed to intrinsic nature of parents especially that of Amol-2, IR50 and Poya, since high yielding hybrids had these parents as male parent. Three hybrids namely IR58025A x Mosa-tarom, IR62829A x Mosa-tarom and IR68899A x Mosa-tarom had significantly negative heterosis and heterobeltiosis, also were low yielding (Table 6). These hybrids had Mosa-tarom as male parent. Therefore Mosa-tarom was found as a weak restorer than that Amol-2, IR50 and Poya.

4. Discussion

The information on the nature of gene action with respective variety and characters might be used depending on the breeding objectives. Investigation of GCA effects revealed that among lines and testers were good general combiners for grain yield and the other traits. Hence these good general combiners of males and females may be extensively used in future for hybrid rice breeding programme. Specific combining ability effect is the index to determine the usefulness of a particular cross combination in the exploitation of heterosis. In the present study, sca effects in six crosses were highly significant and positive for grain yield. Majority of these hybrids involved at least one parent with positive gca effect. Similar results have been reported by Rao et al. (1996). Among the six crosses which depicted highly significant positive sca effects for grain yield, only four crosses (IR68899A/Poya, IR68899A/Amol-2, IR58025A/Poya and IR58025A/IR50) showed high heterosis (Table 6). Dhaliwal and Sharma (1990) reported that non-additive gene effects were predominant for yield and its components. It is evident that cross combinations, which expressed high sca effects for grain yield have invariably exhibited positive sca effects for one or more yield related traits also. While selecting the best specific combination for yield, it would be important to give due weight age to yield related traits. Grafius (1959) had already suggested that there is no separate gene for yield, but yield is an end product of multiplicative interaction among various yield components. In view of this, it appears that heterosis for yield may be through heterosis for individual yield components or alternatively due to multiplication effects of non-additive gene effects of component characters. Generally, high x high, low x high and high x low general combiner parents produced good specific cross combinations. In these crosses additive x additive, dominance x additive and additive x dominance type of gene action was found. In cases, high x high general produced inferior cross combinations indicating epistatic type of gene action for these traits. Six good specific cross combinations (IR58025A x Amol-2, IR58025A x IR50, IR58025A x Poya, IR62829A x Mosa-tarom, IR68899A x Amol-2 and IR68899A x Poya) might be released as hybrid variety for commercial utilization after further study.

Ultimate aim of breeding is to gain the heterotics yield associated with other heterotic characters. Yield is the complex character of all other yield contributing characters. Percent heterosis over mid-parental and better parents were calculated for grain yield and six yield related traits (Table 6). The degree of heterosis varied from cross to cross and from character to character. Pathak and Sanghi (1992) in sorghum and Patel et al. (1994) in upland rice observed the varying degree of heterosis for yield and its related traits. For plant height and days to 50% flowering negative heterosis were desirable but for rest of the characters positive heterosis were desirable. Positive heterosis ranges from 5.74-80.34%; 4.19-15.59%; 5.88-48.74%; 4.56-17.18% and 14.5-106.6% for tiller number, panicle length, spikelets per panicle, spikelet fertility (%) and grain yield, respectively. Negative heterosis ranges from –0.04 to –32.2% and -0.042 to –23.6% for plant height and days to 50% flowering. Watanesk (1993) and Rao et al. (1996) found high heterosis for grain yield and its components in rice. Significantly the highest heterosis (156.6) for grain yield was observed in cross IR68899A x Poya associated with the significant and desirable heterosis for tiller number, plant height and days to 50% flowering. Desirable and significant heterosis for grain yield was found in nine crosses associated with higher heterosis for most of the yield related traits. However, significant and desirable heterosis was observed in nine crosses for tiller number, 10 for plant height, 11 for days to 50% flowering, six for panicle length, 10 for spikelets per panicle and three for spikelet fertility (%). In an ideal situation, hybrids with high tiller number, semi dwarf plant type, short days to 50% flowering, high panicle length, high spikelets per panicle, high panicle fertility and grain yield are preferable. As this situation hardly exists, compromises will have to be made among morphological traits while selecting superior genotypes. Keeping in view mean performance, heterosis and heterobeltiosis estimates, four hybrids (IR68899A x Poya, IR68899A x Amol-2, IR62829A x Poya and IR58025A x IR50) having better mean yield performance are recommended for heterosis breeding.

References

Annadurai, A. & Nadarajan, N. (2001). Combining ability for yield component and physiological traits in hybrid rice. *Madras Agric. J.*, 88: 300-303.

Cockerham, C. C. (1961). Implication of genetic variances in a hybrid breeding programme. *Crop Sci.*, 8: 720-722.

Dhaliwal, T. S. & Sharma, H. L. (1990). Combining ability and maternal effects for agronomic and grain characters in rice. *Oryza*, 27: 122-128.

Faiz, F. A., Sabar, M., Awan, T. H., Tjaz, M. & Manzoor, Z. (2006). Heterosis and combining ability analysis in basmati rice hybrids. *J. Anim. PI. Sci.,* 16 (1 - 2).

Falconar, D. S. & Mackay, T. F. C. (1996). Introduction to Quantitative Genetics. Chapman and Hall. London, U.K.

Fehr, W. R. (1987). Heterosis In: Principles of cultivar development: *Theory and Techniques* (Vol. 1). Macmillan Publishing Company. New York, pp: 115.

Gnansekaran, M., Vivekanandan, P. & Muthuramu, S. (2006). Combining ability and heterosis for yield and grain quality in two line rice (*Oryza sativa* L.) hybrids. *Indian. J. Genet*., 66(1): 6-9.

Grafius, J. E. (1959). Heterosis in barley. *Agron. J.,* 51: 551-554.

Kempthorne, O. (1957). An introduction to genetic statistics. John Wiley and Sons, Inc., New York. pp. 453-471.

Mahto, R. N., Yadava, M. S. & Mohan, K. S. (2003). Genetic variation, character association and path analysis in rainfed upland rice. *Ind. J. Dryland Agric. Res. Dev.*, 18(2): 196-198.

Mishra, L. K. & Verma, R. K. (2002). Genetic variability for quality and yield traits in non-segregating populations of rice (*Oryza sativa* L.). *Plant Archives*, 2(2): 251-256.

Nuruzzamman, M., Alam, M. F., Ahmed, M. G., Shohad, A. M., Biswas, M. K., Amin, M. R. & Hossain, M. M. (2002). Studies on parental variability and heterosis in rice. *Pakisstan Journal of Biological Sciences*, 5 (10): 1006-1009.

Pradhan, S. K., Boss, L. K., & Meher, J. (2006). Studies on gene action and combining ability analysis in Basmati rice. *Journal of Centeral European Agriculture*, Vol. 7 (2): 267-272.

Radish, M., Cheema, A. A. & Ashraf, M. (2007). Line x tester analysis in basmati rice. *Pak. J. Bot.*, 39 (6): 2035-2042.

Ramalingam, J, Nadarajan, N., Vanniyarajan, C., & Rangasamy, P. (1997). Combining ability studies involving cms lines in rice. *Oryza*, 34, P. 4-7.

Rao, A. M., Ramesh, S., Kulkarni, R. S., Savithramma, D. L. & Madhusudhan, K. (1996). Heterosis and combining ability in rice. *Crop Imp*., 23: 53-56.

Rissi, R. D., Hallauer, A. R. & De, R. R. (1991). Evaluation of four testers for evaluating maize lines in a hybrid development program. *Revista Brasllelia de Genetica*, 14: 467-481.

Rogbell, J. E., Subbaraman, N. & Karthikeyan, C. (1998). Heterosis in rice under saline conditions. *Crop Res. Hisar.*, 15: 68-72.

Saleem, M. Y., Mirza, J. I. & Haq, M. A. (2008). Heritability, genetic advance and Heterosis. 2002. In Line x Tester crosses of basmati rice. *J. Agric. Res*., 46 (1): 15-27.

Sarker, U., Biswas, P. S., Prasad, B. & Khaleque Mian, M. A. (2002). Heterosis and genetic analysis in rice hybrid. *Pakistan Journal of Biological Sciences,* 5 (1): 1-5.

Scshu, D. V. (1988). Standard evaluation system for rice. The International Rice Testing Program. The International Rice Research Institute. Los Banos. Philippines. pp. 1-54.

Singh, P. K., Thakur, R., Chaudhary, V. K. & Singh, N. B. (1996). Combining ability for grain yield and its components in relation to rice breeding. *Crop Res. Hisar.*, 11: 62-66.

Surek, H. & Korkut, K. Z. (2002). Heterosis for yield and its components under temperate conditions. Proc. Euro Rice-2001 Symp. Krasnodar, Russia, Sep. 3-8 p: 1-10.

Swati, P. G. & Ramesh, B. R. (2004). The nature and divergence in relation to yield traits in rice germplasm. *Annals. Agric. Res*., 25(4): 598-602.

Vanaja, T. & Babu, L. C. (2004). Heterosis for yield and yield components in rice (*Oryza sativa* L.). *J. Trop. Agri*., 42 (1/2): 43-44.

Verma, O. P., Shanthi, U. S. & Srivastava, H. K. (2002). Heterosis and inbreeding depression for yield and certain physiological traits in hybrids involving diverse ecosystem of rice (*Oryza sativa* L.). *J. Genet. Breed,* 56 (3): 267-278.

Vivek, S., Surendra, S., Singh, S. K. & Singh, H. (2000). Analysis of variability and heritability in new plant type tropical japonica rice (*Oryza sativa* L.). *Environ. Ecol*., 22(1): 43-45.

Watanesk, O. (1993). Heterosis and combining ability evaluation of cytoplasmic male sterile (A) lines and restorer (R) lines. *Int. Rice Res. Not.*, 10: 5-6.

Table 1. Means of the estimated traits for seven parents and 12 F_1 hybrids in rice

Genotypes	Tiller number	Plant height (cm)	Days to 50% flowering	Panicle length (cm)	Number of spikelets per panicle	Spikelet fertility (%)	Grain yield per 10 plants (gr)
Lines							
1. IR58025A	16.33 b	74.40 a	79.30 a	24.37 a	233.34 a	0.00 a	†414.50 a
2. IR62829A	19.70 a	63.66 b	70.70 b	20.80 b	145.33 b	0.00 a	380.50 c
3. IR68899A	19.30 a	65.33 b	65.34 c	21.66 b	180.40 b	0.00 a	392.07 b
Testers							
4. Amol2	23.33 a	101.70 c	69.00 a	23.52 c	143.33 b	93.70 a	411.03 b
5. IR50	18.67 b	100.34 c	69.00 a	28.63 b	260.67 a	74.06 c	455.17 a
6. Poya	10.40 c	144.66 b	61.33 c	30.87 b	237.00 a	85.64 b	263.30 d
7. Moosa-tarom	17.70 b	186.70 a	64.00 b	37.13 a	163.00 b	91.59 ab	286.03 c
Hybrids							
1 x 4	18.33 g	101.66 g	61.33 g	28.17 defg	233.00 c	82.20 b	565.20 e
1 x 5	33.67 a	103.7 fg	63.00 e	31.33 bc	276.00 ab	86.79 ab	605.50 d
1 x 6	22.40 def	120.16 d	70.00 b	30.57 bcd	285.33 ab	71.60 c	571.37 e
1 x 7	13.70 h	130.36 b	71.00 a	41.33 a	298.00 a	19.75 e	87.27 i
2 x 4	25.30 bc	91.33 h	60.67 h	25.90 g	200.00 d	85.98 ab	540.80 f
2 x 5	32.00 a	83.66 i	62.00 f	25.63 g	292.00 ab	81.61 b	521.20 g
2 x 6	28.33 b	104.50 f	54.00 j	27.20 efg	279.00 ab	89.55 a	628.30 c
2 x 7	19.30 fg	126.50 c	70.67 a	32.20 bc	205.67 d	68.12 c	312.77 h
3 x 4	24.67cde	92.17 h	53.00 k	26.53 fg	232.00 c	90.00 a	661.30 b
3 x 5	22.00 def	93.17 h	57.00 i	29.83 cde	280.67 ab	58.21 d	521.27 g
3 x 6	26.30 bc	110.00 e	54.00 j	29.33 cdef	236.33 c	84.22 ab	809.93 a
3 x 7	21.67 ef	135.00 a	68.00 d	33.33 b	268.33 b	19.84 e	73.13 j

In each column, any two means having a common letter are not significantly different at $p = 0.05$ based on Duncan's Multiple Range Test.

†: Grain yield of maintainer lines for related CMS lines.

Table 2. Analysis of variance for combining ability effects of different traits in rice

Sources of variation	df	MS						
		Tiller number	Plant height (cm)	Days to 50% flowering	Panicle length (cm)	Number of spikelets per panicle	Spikelet fertility (%)	Grain yield per 10 plants (gr)
Replication	2	5.89 ns	5.43 ns	0.123 ns	0.14 ns	480.75 ns	58.45**	33.14 ns
Genotypes	18	102.4**	2609.6**	145.7**	77.11**	7322.1**	3640.3**	106933.7**
Parents (p)	6	47.5**	6248.8**	102.0**	102.8**	6950.2**	6493.2**	14958.6**
P vs C	1	488.0**	79.85**	530.7**	153.4**	51776.3**	5595.0**	190046.3**
Crosses (c)	11	97.3**	854.53**	134.5**	56.15**	3478.4**	1906.6**	149543.6**
Lines	2	36.77**	468.23**	208.8**	79.67**	2582.2**	1200.9**	11241.3**
Testers	3	204.2**	2702.6**	253.7**	130.3**	6049.3**	4769.8**	468269.9**
L x T	6	64.1**	59.27**	50.22**	11.22**	2491.7**	710.2**	36281.2**
Error	36	2.60	2.75	0.12	1.91	234.81	9.53	15.9
δ^2_{gca}	6	1.43 ns	34.3**	3.64**	1.94 ns	42.56**	51.6**	4885.83**
δ^2_{sca}	11	20.49**	18.83**	16.70**	3.103**	752.28*	233.546*	12088.40**
$\delta^2_{gca} / \delta^2_{sca}$	-	0.069	1.82	0.217	0.62	0.056	0.22	0.407
CV (%)		9.21	1.24	0.53	4.60	7.62	3.58	1.13

* and **; Significant at p = 0.05 and p = 0.01 levels, based on an F-test, respectively.

Ns: non-significant.

Table 3. Proportional contribution of lines, testers and their interactions to total variance in rice

Source	Tiller number	Plant height (cm)	Days to 50% flowering	Panicle length (cm)	Number of spikelets per panicle	Spikelet fertility (%)	Grain yield per 10 plants (gr)
Due to line	6.87	9.96	28.21	25.79	13.49	11.45	1.37
Due to tester	57.22	86.25	51.42	63.30	47.43	68.23	85.39
Due to line x tester	35.91	3.78	20.36	10.90	39.07	20.32	13.23

Table 4. General combining ability (g_i) effects for traits in rice parents

traits Genotype	Tiller number	Plant height (cm)	Days to 50% flowering	Panicle length (cm)	Number of spikelets per panicle	Spikelet fertility (%)	Grain yield per 10 plants (gr)
Lines							
1. IR58025A	-1.72	6.30**	4.28**	2.74*	15.89	-4.73*	-34.16**
2. IR62829A	1.78	-6.19**	-0.22	-2.37*	-13.02	11.49**	9.27*
3. IR68899A	-0.05	-0.08	-4.05**	-0.35	-2.85	-6.75*	24.91**
SE (g_i)	0.46	0.48	0.101	0.39	4.42	0.89	1.15
Testers							
4. Amol-2	-1.94*	-12.61**	-3.72**	-3.24**	-35.52**	16.24**	97.6**
5. IR50	5.50**	-14.13**	-1.39**	-1.17	25.69*	5.72*	57.82**
6. Poya	1.95*	3.88**	-2.72**	-1.07	9.69	11.97**	178.36**
7. Mosa-tarom	-5.49**	22.95**	7.83**	5.51**	0.14	-33.91**	-333.77**
SE (g_i)	0.53	0.55	0.12	0.46	5.10	1.03	1.328

* and ** General combining ability estimate significantly different from zero at p = 0.05 and 0.01, respectively, based on an T-Test.

Table 5. Specific combining ability (s_{ij}) effects for traits in rice crosses

traits Crosses	Tiller number	Plant height (cm)	Days to 50% flowering	Panicle length (cm)	Number of spikelets per panicle	Spikelet fertility (%)	Grain yield per 10 plants (gr)
1 x 4	-1.72	0.29	-1.28**	-1.44	-4.56	0.87	10.26**
1 x 5	6.16**	3.91**	-1.94**	-0.34	-22.7**	15.98**	90.34**
1 x 6	-1.61	2.29*	6.39**	-1.206	2.55	-5.45*	64.33**
1 x 7	-2.83*	-6.58**	-3.17**	2.97**	24.77*	-11.42**	-36.28**
2 x 4	-1.22	2.45*	2.55**	1.41	-8.64	-11.57**	-57.56**
2 x 5	0.99	-3.69**	1.55**	-0.92	22.13*	-5.42*	-37.38**
2 x 6	0.88	-0.88	-5.11**	0.54	25.13*	-3.74	-50.83**
2 x 7	-0.67	2.05	0.99**	-1.04	-38.64**	20.71**	145.77**
3 x 4	2.94**	-2.80*	-1.28**	0.02	13.19	10.68**	47.29**
3 x 5	-7.17**	-0.28	0.39	1.25	0.63	-10.57**	-52.96**
3 x 6	0.72	-1.47	-1.28**	0.65	-27.69**	9.18**	115.16**
3 x 7	3.49**	4.46**	2.17**	-1.94*	13.85	-9.31**	-109.45**
SE (s_{ij})	0.93	0.96	0.202	0.79	8.84	1.78	2.30

* and ** General combining ability estimate significantly different from zero at p = 0.05 and 0.01, respectively, based on an T-Test.

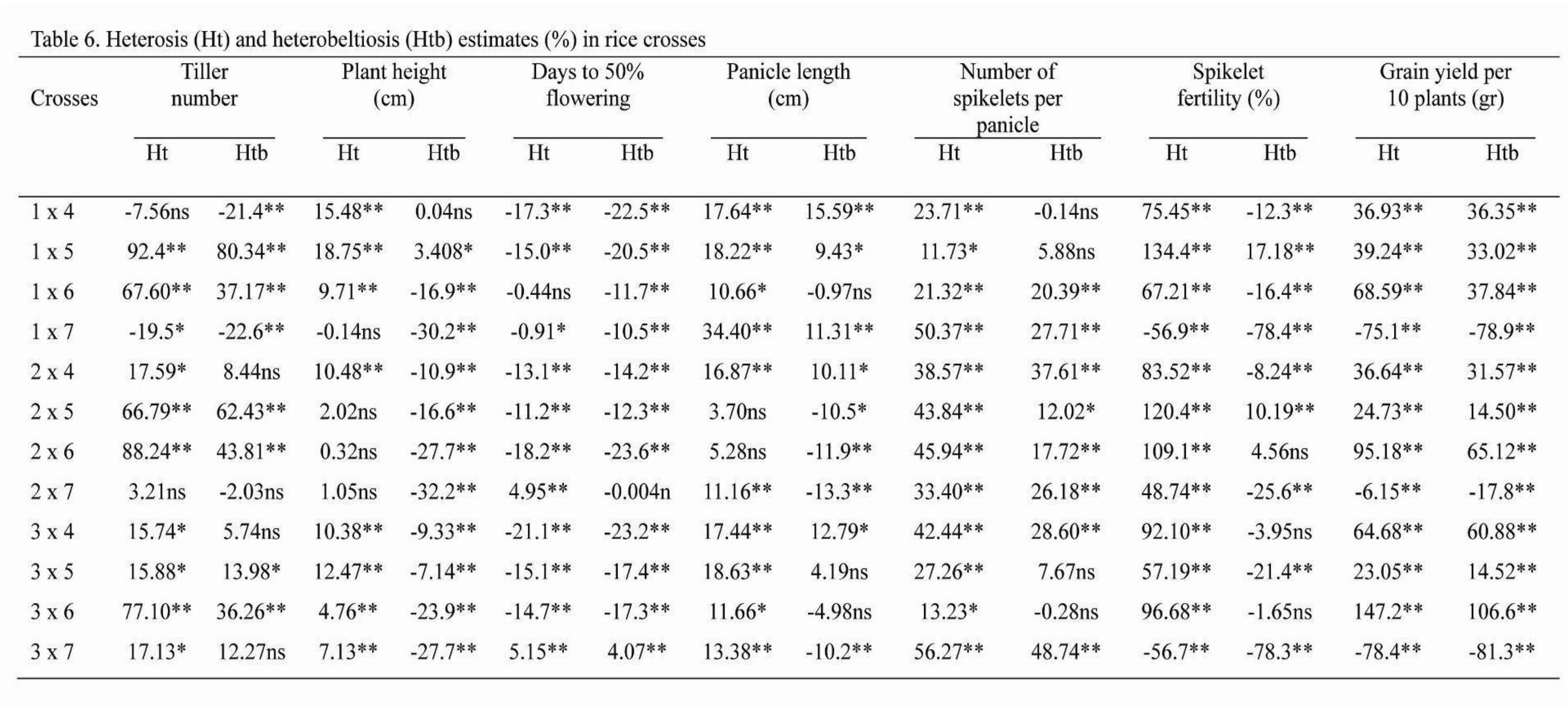

Table 6. Heterosis (Ht) and heterobeltiosis (Htb) estimates (%) in rice crosses

Crosses	Tiller number		Plant height (cm)		Days to 50% flowering		Panicle length (cm)		Number of spikelets per panicle		Spikelet fertility (%)		Grain yield per 10 plants (gr)	
	Ht	Htb	Ht	Htb	Ht	Htb	Ht	Htb	Ht	Htb	Ht	Htb	Ht	Htb
1 x 4	-7.56ns	-21.4**	15.48**	0.04ns	-17.3**	-22.5**	17.64**	15.59**	23.71**	-0.14ns	75.45**	-12.3**	36.93**	36.35**
1 x 5	92.4**	80.34**	18.75**	3.408*	-15.0**	-20.5**	18.22**	9.43*	11.73*	5.88ns	134.4**	17.18**	39.24**	33.02**
1 x 6	67.60**	37.17**	9.71**	-16.9**	-0.44ns	-11.7**	10.66*	-0.97ns	21.32**	20.39**	67.21**	-16.4**	68.59**	37.84**
1 x 7	-19.5*	-22.6**	-0.14ns	-30.2**	-0.91*	-10.5**	34.40**	11.31**	50.37**	27.71**	-56.9**	-78.4**	-75.1**	-78.9**
2 x 4	17.59*	8.44ns	10.48**	-10.9**	-13.1**	-14.2**	16.87**	10.11*	38.57**	37.61**	83.52**	-8.24**	36.64**	31.57**
2 x 5	66.79**	62.43**	2.02ns	-16.6**	-11.2**	-12.3**	3.70ns	-10.5*	43.84**	12.02*	120.4**	10.19**	24.73**	14.50**
2 x 6	88.24**	43.81**	0.32ns	-27.7**	-18.2**	-23.6**	5.28ns	-11.9**	45.94**	17.72**	109.1**	4.56ns	95.18**	65.12**
2 x 7	3.21ns	-2.03ns	1.05ns	-32.2**	4.95**	-0.004n	11.16**	-13.3**	33.40**	26.18**	48.74**	-25.6**	-6.15**	-17.8**
3 x 4	15.74*	5.74ns	10.38**	-9.33**	-21.1**	-23.2**	17.44**	12.79*	42.44**	28.60**	92.10**	-3.95ns	64.68**	60.88**
3 x 5	15.88*	13.98*	12.47**	-7.14**	-15.1**	-17.4**	18.63**	4.19ns	27.26**	7.67ns	57.19**	-21.4**	23.05**	14.52**
3 x 6	77.10**	36.26**	4.76**	-23.9**	-14.7**	-17.3**	11.66*	-4.98ns	13.23*	-0.28ns	96.68**	-1.65ns	147.2**	106.6**
3 x 7	17.13*	12.27ns	7.13**	-27.7**	5.15**	4.07**	13.38**	-10.2**	56.27**	48.74**	-56.7**	-78.3**	-78.4**	-81.3**