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Heterosis and Combining Ability Studies for yield and Productivity Traits in Rice: A Review

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A review of work done was undertaken for accessing the extent of heterosis, general and specific combining ability for yield and productivity traits in rice. Identification of genetically superior parents is an important prerequisite in for the development of hybrids in rice. The combining ability analysis has been the efficient tool in choosing the desirable parents for hybridization programmes. It provides an empirical summary of complex observations and makes it possible to classify the parental lines in terms of superiority in hybrid combinations and the gene action involved in the inheritance of different traits. In majority of the experiments high specific combining ability (SCA) variances than general combining ability (GCA) variances for most of the traits were reported which indicate the predominance of non-additive gene action in the inheritance of these traits. However, in many other experiments the significance of GCA and SCA variances were also reported, and thus the equal importance of both additive and non-additive genetic components have been described. The researchers also found some correspondence between good general combiners and *per se* performance for some of the traits. Therefore, analysis of combining ability has been the most important and efficient tool in selecting the desirable parents for a hybridization programme. This review will help in understanding the exciting opportunities offered by heterosis, combining ability and gene action studies in rice.

Key words: Rice, Heterosis, Combining ability, Gene action.

INTRODUCTION

Rice (*Oryza sativa* L., 2n = 24) is one of the major staple food crop being grown worldwide. It is the staple food for more than half of the world's population. It is a nutritious cereal crop, provides 20 per cent of the calories and 15 per cent of protein consumed by world's population. Besides being the chief source of carbohydrate and protein in Asia, it also provides minerals and fibre. India has an area of 43.66 million hectares under rice cultivation with production of 91.79 million tones, with productivity of 2.10 tones ha^{-1}. Dietary intake surveys from China and India reveal that an average adult intake is about 300 g of raw rice per day. The country witnessed an impressive growth in rice production in the post-independence era due to the adoption of semi-dwarf high yielding varieties coupled with the intensive input based management practices. Rice production was increased four times, productivity three times while the area increase was only one and half times during this period. In order to keep pace with the growing population, the estimated rice requirement by 2025 is about 130 m tonnes. Plateauing trend in the yield of HYV's, declining and degrading natural resources like land and water and acute shortage of labor make the task of increasing rice production quite challenging. Among several options besides crop management, the innovative genetic option of hybrid rice technology is practically feasible and readily adoptable (Viraktamath *et al*., 2010). Hybrids play an important role in enhanced yield production by heterosis breeding. Developing rice hybrids for both aerobic and drought prone situation is extremely essential to maintain the yields of rice for the present and the near future to keep the rice production sustainable for the growing population with the available depleting water resources. Hybrid rice is practically feasible and readily adoptable genetic option to increase rice production and has been amply demonstrated in China and India.

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Hybrid rice technology is recently deployed approach to increase yield through exploitation of heterosis, the success is already being experienced in China, India and elsewhere. Availability of effective male sterility and fertility restoration system is one of the essential pre requisites for commercial exploitation of heterosis. The decade of 1960s has been an eventful for rice research and development. The semi dwarf rice varieties revolutionized the rice production worldwide. In the same period professor Yuan Long Ping acknowledge as Father of Hybrid Rice began his pioneering research on hybrid rice in China during 1964. Arduous efforts of Prof Yuan Long Ping and his associates resulted in development and identification of heterotic rice hybrids. First commercial three-lines rice hybrid developed in China during 1974. Hybrid rice was released for large scale cultivation and commercialization in china during 1976. The research on hybrid rice was reviewed by Dr. Virmani at IRRI with help of Chinese CMS lines since the Chinese CMS lines were unadapted and highly susceptible to disease and pests under tropical conditions. Dr. Virmani developed several new CMS lines adapted to tropics utilizing the WA cytoplasm from Chinese CMS lines V20A and Zenshan-974. The most successful among them include IR-58025 A and IR 62829A. Yield superiority of rice hybrid in tropics was confirmed by IRRI in 1982. Out of the 20 countries engaged in hybrid rice research and development, hybrid rice was already commercialized in 10 countries including the china as first followed by Vietnam and India. Though the area grown to hybrid rice is still very limited in all these countries except in china where hybrid rice is grown in 15.5 million ha. In India hybrid rice programme was started during 1990s with IRRI and is being grown in 2 million ha. As a result of concerted efforts for over two decades, totally 46 hybrids have been released for commercial cultivation in the country. Among 46 hybrids, 29 have been released from public sector while remaining 17 have been developed and released from private sector. Though 46 hybrids have been released in the country so far, some of them have been outdated, and some are not in the production chain, so there is still more scope to develop hybrid rice for increasing rice productivity (Veeresha, 2012). Performance of a F_1 hybrid depends on choice of parents. Several methods like *per se* performance, genetic diversity, combining ability etc., have been attempted to select the parents. Among them combining ability analysis offers a powerful tool for estimating the value of a parent to produce superior hybrid. The knowledge of combining ability is useful to assess nicking ability among genotypes and at the same time elucidate the nature and magnitude of gene actions involved. Breeders use these variance components to measure the gene action and to assess the genetic potentialities of parent in hybrid combinations. Among the several statistical tools available to detect the combining ability and gene action governing various quantitative traits, diallel (Griffing, 1956) and line x tester (Kempthorne, 1956) matting designs provide reliable information about the general and specific combining abilities (GCA and SCA) of parents and their cross combinations and are helpful in estimating various types of gene actions. It is also necessary to assess the genetic potential of parents in hybrid combination through systematic studies in relation to both general and specific combining abilities, which could be attributed to additive and non-additive components of gene action, respectively. Here we are taking a review of work done by different scientists for accessing the extent of heterosis, gene action, general and specific combining ability in rice at individual as well as over environments.

Terminologies used in the study

Heterosis: The term heterosis was given by Shull (1914). It refers to the superiority / inferiority of the F_1 over its parents with respect to yield, size, number etc.

Average Heterosis: It refers to superiority of the F_1 over mid parents with respect to yield, size, number etc.

Heterobeltiosis: It refers to superiority of the F_1 over better parent with respect to yield, size, number etc.

Standard heterosis: It refers to superiority of the F_1 over the commercial check with respect to yield, size, number etc.

Combining Ability: The concept of combining ability was introduced by Sprague and Tatum (1942). It is the capacity of a genotype to transmit superior performance to its crosses. It is categorize as General combining ability (GCA) and specific combining ability (SCA).

General Combining Ability (GCA): Is the relative ability of a biotype / genotype to transmit desirable performance to its crosses. According to Sprague and Tatum general combining ability (GCA) is the average performance of a strain / genotype in a series of crosses. It is a measure of additive gene action.

Specific Combining Ability (SCA): The term specific combining ability (SCA) is used to designate those cases in which certain combinations do relatively better / worse than what is expected on the basis of average performance of lines involved. It is the performance of a genotype in a specific cross. It is a measure of non-additive gene action.

Additive Gene Action: Joint effect of additive variance plus additive x additive type of epistasis.

Non-additive Gene Action: Joint effect of dominance and additive x dominance and dominance x dominance type of epistasis.

Heterosis and combining ability for productivity traits

Heterosis in rice was first reported by Jones in 1926 who observed a marked increase in Culm number and grain yield in some F_1 hybrids in comparison to their parents. Heterosis refers to the superiority / inferiority of the F_1 hybrid over the mean parental value (mid parent heterosis) or the better parent (heterobeltiosis) or the best commercial variety (standard heterosis). the studies done by different scientists with respect to heterosis and combining ability for different productivity traits in rice has been reviewed trait wise as under.

Days to 50 per cent flowering

Ganasekaran *et al*. (2006) observed that the hybrids GD 98049/IR 72 was found significantly heterotic over standard check. Malini *et al*. (2006) observed significantly negative heterobeltiosis as well as standard heterosis for days to flowering. Nadali (2011) observed significant negative mid-parent and high parent heterosis. The results were in agreement with Sunil Kumar *et al*. (2012). Significant heterosis for earliness was reported by Patil *et al*. (2011). Similar results were obtained by Sarial *et al*. (2006), Raj *et al*. (2007) and Venkateshan *et al*. (2008) reported that based on the gca effects of parents, the line IR 58029-99-3-1-3 and tester BR 4828-2-2-1 recorded negative gca effects for days to 50 per cent flowering. Swamy *et al.* (2003) identified GMR 17 as the best general combiner for earliness. Tiwari *et al*. (2011) observed highly GCA effects for this trait.

Plant height

The heterosis in plant height might introduce the problem of lodging and many scientists noted the importance of parental selection. High magnitude of heterobeltiosis and standard heterosis were observed by Akarsh and Pathak (2008). Negative heterosis for plant height is desirable for breeding short statured hybrids and varieties. Patil *et al*. (2011) reported negative heterosis over better parent up to 15.97 percent. The results were in close association with results of Yadav *et al*. (2004), Datt and Mani *et al*. (2004), Raju *et al*. (2006) and Parihar and Pathak (2008). Similarly Sunil Kumar *et al*. (2012) also reported highly significant negative heterosis over better parent and mid parent. Tiwari *et al*. (2011) observed significant heterobeltiosis and reported from heterobeltiosis and reported from his study that none of the cross combinations were common for both the heterosis, suggesting that hetsrosis for plant height is cross specific. These finding were in close association with results of Peng and Virmani (1991), Nuruzzaman *et al*. (2002), Alam *et al*. (2004). Muhammad Rashid *et al*. (2007) reported negative and highly significant GCA and SCA effects. The similar observations were made by Won and Yoshida (2000), Roy and Mandal (2001), Sarker *et al*. (2002). Swamy *et al. (*2003) identified the new CMS line IR 70370A as good general combiner for plant height.

Number of panicles per plant (Number of productive tillers)

Akarsh and Pathak (2008) reported high magnitude of heterobeltiosis and standard heterosis for effective tillers per plant these results are in agreement with Ganasekaran *et al*. (2006). Patil *et al*. (2011) reported significant result for heterobeltosis, up to 30.45 %. Pandya and Tripathi (2006), Eradasappa *et al*. (2007) and Parihar (2008) also reported similar results. Tiwari *et al*. (2011) and Sunil Kumar *et al*. (2012) reported significant desirable heterosis over better parent and mid parent. Muhammad Rashid *et al*. (2007) reported the highly significant GCA effects, the similar results were reported by Singh and Kumar (2004), Roy and Mandal (2001), Sarker *et al*. (2002). Highly significant and SCA effects for these traits were reported by Muhammad Rashid *et al.* (2007).

Panicle length

Ganasekaran *et al*. (2006) observed that the hybrids GD 98049/IR 72 was found significantly heterotic over standard check for panicle length. Similarly Malini *et al*. (2006) reported standard heterosis and heterobeltiosis for this trait in the hybrid combination IR 68885A / White ponni. Patil *et al*. (2011) reported significant result for heterobeltosis in desirable direction up to 24.06 percent. These were in confirmation with the results reported by Patil *et al*. (2003), Yadav *et al*. (2004), Dutta and Mani *et al*. (2004) and Pandya and Tripathi (2006). Tiwari *et al*. (2011) observed as well as negative heterosis of panicle length. Nadali Bagheri (2010) reported significant and mid parent heterosis but non-significant heterobeltosis manifesting partial dominant type of gene action. Muhammad Rashid *et al*. (2007) reported highly significant GCA and SCA effects. These results were in agreement with findings of Chen *et al*. (1995). The significant high SCA effects was reported by Pradeep Kumar and Reddy C.V.C.M. (2011), similar results were reported earlier by Virmani (1994). Veni and Rani (2003) reported that the panicle length exhibited significant specific combining ability (SCA) variances.

Number of spikelets per panicle

Malini *et al*. (2006) reported standard heterosis and heterobeltiosis for spikelets per panicle in the hybrid combination IR 68885A / White ponni. Veni and Rani (2003) reported that total spikelets per panicle exhibited significant general combining ability (GCA) effects. Swamy *et al.* (2003) identified the new CMS line IR 70370A as good general combiner for filled spikelets per panicle and IRBPHN 89 among the testers.

Spikelet fertility

Ganasekaran *et al*. (2006) observed that the hybrids GD 98049/IR 72 was found significantly heterotic over standard check for spikelet fertility. Tiwari *et al*. (2011) reported the significant heterobeltosis and standard heterosis for this character. The range heterosis over better parent and standard variety varied from 6.89 to 16.3 percent. Veni and Rani (2003) reported that the variance, due to general combining ability (GCA) effects were significant for sterility percentage. Swamy *et al. (*2003) identified IRBPHN 89 as the best general combiner for spikelet fertility per cent among the testers and CMS line IR 70370A among the lines. Sunil Kumar *et al*. (2011) reported the significant negative heterosis over better parent and mid parent. Pradeep Kumar and Reddy C.V.C.M. (2011), Tiwari *et al*. (2010) reported significant SCA effect for this trait. The good general combiners for this character were IR628229, Amol-2, IR 50, and Poya as reported by Tiwari *et al*. (2010).

Grain yield per plant

High heterosis in grain yield was due to simultaneous heterosis in one or more yield components as reported by Virmani *et al*. (1981, 1982). Rajesh Singh (2000) reported the significant heterosis for grain yield. Malini *et al*. (2006) reported relative heterosis for grain yield per plant ranged between -69.17 to 243.21 coupled with significant heterobeltiosis from -75.71 to 219.75. The standard heterosis ranged from -73.71 to 129.16 for grain yield per plant. Similarly Akarsh and Pathak (2008), Saravanan *et al.* (2008) reported high magnitude of heterobeltiosis and standard heterosis. Tiwari *et al*. (2011) reported the standard heterosis as high as 30% in his study. Similar findings were reported by Virmani *et al*. (1981), Nuruzzaman *et al*. (2002), Li *et al*. (2002), Faiz *et al*. (2006), Saleem *et al*. (2008), Rahimi *et al*. (2010). Veni and Rani (2003) reported that the variance, due to general combining ability (GCA) and SCA effects were significant for grain yield per plant. Shanthi *et al*. (2003) revealed that the lines IR58025A, PMS3A and the restorer IR65514R as good combiners for grain yield and most of the associated traits and the crosses IR58025A/IR65514R, IR58025A/IR42266R, PMS3A/IR29341 and PMS3A/IR50404R were identified as superior combinations. Swamy *et al.* (2003) identified the new CMS line IR 70370A, Pradhan *et al*. (2006) reported the female CMS line IR68281A and the male parental lines, Taraori Basmati, Pusa 2503-693-1, Pusa 1235-95-73-1 and Pusa 2512-97-83-98-4 as best general combiners for grain yield. Based on GCA effects, the parents IR 58025 A (WA source line), G 46 A (Gambiaca source line), Ratnagiri 3, IR 46, IR 54 and IR 5 (testers) were identified as good general combiners for yield and its component characters by Sawant *et al*. (2006). Nadali (2010) observed the highly significant SCA effects for grain yield. Muhammad Rashid *et al*. (2007) reported predominant non additive gene action for grain yield in his study. These results agreed with the results of Pradeep Kumar and Reddy C.V.C.M. (2011). The better general combiners for grain yield have been reported by many workers for grain yield as punished in Table 1.

Table 1. Rice cultivars identified as good general combiners for yield

Good combiner	Origin	Reference
IR 58025A, PMS 3A and IR 65514R	India	Shanthi *et al*. (2003)
IR 70370A, IRBPHN 89	India	Swamy *et al*. (2003)
Vyttila	India	Vanaja *et al*. (2003)
IET 13846, Kasturi, Basmati 370, Toraoti Basmati, Pusa Basmati and IR 64-	India	Panwar *et al*. (2005)
IR 69616, Basmari 385	India	Faiz *et al*. (2006)
Toraoti Basmati, Pusa 2503-693-1, IR 68281A, Pusa 1235-97-83-98-4, Pusa 2512-97-83-98-4	India	Pradhan *et al*. (2006)
IR 58025A, 64A, Patnagiri, IR 64, IR 54, IR 5	India	Sawant *et al*. (2006)
Super Basmati, DM-25, DM-107-4	India	Muhammad *et al*. (2007)
ASD 6, ADT 38, CB 98002, CD 98006	India	Senguttuvel and Kannan (2007)
DMS 10A, BR 827-35-K2, IR 53480	India	Mehla *et al*. (2008)
Kasturi, Basmati 5853, Hryana Basmati, Panthdhan	India	Sharma and Mani (2008)
Poya, IR 62829A	India	Nadali (2010)
IR 58025A, IR 68897A and IR 79156A	India	Veeresha *et al*. (2013)

Thousand grain weight

Akarsh and Pathak (2008) reported high magnitude of heterobeltiosis and standard heterosis for 1000 grain weight. Significant and negative heterosis over better parent and mid parents was observed by Sunil Kumar *et al*. (2011). Similar findings were made by Rosanama and Vijayakumar (2005). The extent of heterosis for grain weight was - 41.25 % to 71.63% over better parent and from - 43.25% to 21.81 % over standard variety as reported by Tiwari *et al*. (2011). Virmani *et al.* (1981, 1982) reported heterosis in yield was mainly due to heavier 1,000-grain weight. Veni and Rani (2003) reported that the test weight exhibited significant specific combining ability (SCA) variances. Muhammad Rashid *et al*. (2007) reported significant GCA and SCA effects. These results were in line with the findings of Roy and Mandal (2001), Singh and Kumar (2004), Pradeep Kumar and Reddy (2011) reported significant and desirable SCA effects.

Grain L/B ratio

Ganasekaran *et al*. (2006) observed that the hybrids GD 98049/IR 72 was found significantly heterotic over standard check IR 72 for kernal L/B ratio and kernel elongation on cooking. Patil *et al*. (2011) noticed highly significant heterosis over better parent in desirable direction. Similar observations made by Venkatesan *et al*. (2008).

Days to maturity

Malini *et al*. (2006) observed significantly negative heterobeltiosis as well as standard heterosis for maturity in most of the hybrids indicating the possibility of exploiting heterosis for earliness.

Grains per panicle

Ganasekaran *et al*. (2006) observed that the hybrids GD 98049/IR 72 was found significantly heterotic over standard check. Patil *et al*. (2011) reported significant heterotic effects over better parent, the results were in agreement with the findings of Patil *et al*. (2003) and Pandya and Tripathi (2006). Tiwari *et al*. (2011) reported the significant and negative heterosis over better parent and standard variety. These observations were in agreement with Sunil Kumar *et al*. (2011), Eradasappa *et al*. (2007) and Rosanama and Vijayakumar (2005). Veni and Rani (2003) revealed that the variance, due to general combining ability (GCA) effects were significant for fertile grains per panicle. Pradeep Kumar and Reddy C.V.C.M. (2011) reported significant SCA effects and said that non additive effects were predominant. Significant GCA and SCA effects were observed by Mirarab *et al*. (2011).

This shows the contribution of both additive and non additive effects in genetic control of this trait. From the practical point of view, standard heterosis is the more important of the two levels of heterosis because it is aimed at developing desirable hybrids superior to the existing high yielding commercial varieties (Chaudhary, 1984). Significant positive as well as negative heterosis, heterobeltiosis and standard heterosis have been reported in rice by number of workers for yield and productivity traits as presented in Table 2. Presence of heterosis and specific combining ability (SCA) effects for yield and yield related traits in rice hybrids were reported by Young and Virmani (1990). To exploit maximum heterosis using male sterility system in hybrid breeding programme, we must know the combining ability of different male sterile and restorer lines. The general combining ability (GCA) refers to the average performance of a particular inbred in a series of hybrid combinations, where as the performance of two specific inbreds in particular cross combination

Table 2. Summary of range of heterosis reported for yield and productivity traits in rice

Character	Heterosis		Reference
	Standard heterosis	Heterobeltiosis	
Days to 50% flowering	Negative		Malini *et al.* (2006), Veeresha *et al.* (2013a)
	Positive		Bisne *et al.* (2008), Malrvizhi *et al.* (2009)
		-23.60 to4.07	Nadali Bagheri (2010)
	-4.22 to -16.57	-16.57 to 7.27	Tiwari *et al.* (2011)
		-14.97 to 13.63	Patil *et al.* (2011)
		-8.36 to 2.88	Sunil Kumar *et al.* (2012)
Plant height		-14.67 to 1084	Sarker *et al.* (2002)
		-13.48 to 0.35	Faiz *et al.* (2006)
		3.25 to 42.99	Saleem *et al.* (2008)
		-32.20 to 3.41	Nadali Bagheri (2010)
	-8.30 to 60.90		Rahimi *et al.* (2010)
	-19.62 to 0.18	-16.99 to 8.29	Tiwari *et al.* (2011)
		-15.97 to 15.09	Patil *et al.* (2011)
		-23.56 to -8.49	Sunil Kumar *et al.* (2012)
Number of Panicles/ plant	Positive		Singh *et al.* (2002), Anand and Singh (2002), Ganasekaran (2006), Munnisonnappa and Vidyachandra (2007), Veeresha *et al.* (2013a)
		-37.50 to 11.40	Faiz *et al.* (2006)
	-19.00 to 31.00		Bisne *et al.* (2008)
	-16.00 to 34.00		Saravanan (2008)
	-38.70 to 13.60		Rahimi *et al.* (2010)
	-8.330to 66.67	-34.00 to 39.53	Tiwari *et al.* (2011)
		-30.69 to 30.45	Patil *et al.* (2011)
		-30.56 to 22.22	Sunil Kumar *et al.* (2012)
Panicle Weight		-39.27 to 56.41	Sarker *et al.* (2002)
	Positive		Gunaskaran (2006)
Panicle length	Positive		Anand and Singh (2002), Vanaja and Babu (2004), Khoyumthem *et al.* (2005)
		Positive	Bisne *et al.* (2008), Narasimman *et al.* (2007), Saravanan (2008)
		-13.30 to 15.59	Nadali Bagheri (2010)
	-14.90 to 6.90		Rahimi *et al.* (2010)
		-14.24 to 24.06	Patil *et al.* (2011)
	-40.63 to23.20	-39.26 to 48.30	Tiwari *et al.* (2011)
		-80.47 to 7.39	Faiz *et al.* (2006)
	-25.10 to 10.80		Rahimi *et al.* (2010)
		-26.34 to 20.78	Patil *et al.* (2011)
	-16.86 to 21.02	-20.66 to 46.61	Tiwari *et al.* (2011)
Spikelet fertility		-57.62 to 66.11	Sarker *et al.* (2002)
	Positive		Ganasekaran (2006), Munnisonnappa and Vidyachandra (2007)
		64.45%	Manojkumar (2008)
		-78.40 to 17.18	Nadali Bagheri (2010)
	-0.81 to 16.31	-6.89 to 46.40	Tiwari *et al.* (2011)
		-36.24 to 10.89	Sunil Kumar *et al.* (2012)
Grain yield	Positive		Rajesh Singh (2000), Durai (2002), Kshirsagar *et al.* (2005), Ganasekaran (2006), Munnisonnappa and Vidyachandra (2007), Bisne *et al.* (2008), Rishika Sharma and Malik (2008), Venkatesan *et al.* (2008)
	60.00 %		Singh *et al.* (2002)
		-48.49 to 100.70	Sarker *et al.* (2002)
	-91.16 to 111.28		Anand and Singh (2002)
	18.00 to 40.00		Malarvizhi *et al.* (2003)
		-87.95 to 41.83	Faiz *et al.* (2006)
	-73.70 to 129.16	-75.71 to 219.75	Malini *et al.* (2006)
	Positive	Positive	Narasimman *et al.* (2007), Manojkumar (2008)
		64.95 %	Saravanan (2008)
		-6.97 to 66.38	Saleem *et al.* (2008)
		-6.97 to 66.38	Saleem *et al.* (2008)
		-22.43 to 47.05	Patil *et al.* (2011)
		-39.59 to 6.04	Sunil Kumar *et al.* (2012)

Continue……………………

1000 Seed weight	Positive		Anand and Sing (2002), Singh *et al.* (2002), Vanaja *et al.* (2003), Ganasekaran (2006), Munnisonnappa and Vidyachandra (2007), Bisne *et al.* (2008)
		Positive	Khoyumthem *et al.* (2005)
	-4.60 to 18.10		Rahimi *et al.* (2010)
		-21.86 to 35.89	Patil *et al.* (2011)
		-36.24 to 10.89	Sunil Kumar *et al.* (2012)
L/B ratio	Positive		Ganasekaran (2006), Venkatesan *et al.* (2008)
		-22.92 to 16.61	Patil *et al.* (2011)
Days to Maturity		Positive	Khoyumthem *et al.* (2005)
		-5.34 to 2.80	Sunil Kumar *et al.* (2012)
No of Spikelets per panicle	-20.00 to 6.00		Cho *et al.* (1994)
		Positive	Lingaraju *et al.* (1999), Khoyumthem *et al.* (2005), Munnisonnappa and Vidyachandra (2007)
	Positive		Anand and sing (2002), Vanaja and Babu (2004)
		-40.38 to 36.98	Faiz *et al.* (2006)
		-0.28 to 17.18	Nadali Bagheri (2010)
	-33.56 to 12.08	-40.44 to 8.56	Tiwari *et al.* (2011)

Table 3. Gene action and combining ability in rice

Character	Additive (GCA)	Non additive (SCA)	Additive and Non additive
Days to 50% flowering	Swamy *et al.* (2003)		Faiz *et al.* (2006)
Plant height	Swamy *et al.* (2003) , Vanaja *et al.* (2003), Senguttuvel and Kannan (2007)	Akarsh and Pathak (2008), Haripresanna *et al.* (2006), Pradhan (2006), Umakanta (2002).	Mahamad Rashid (2007), Zhao (2008), Sing (2005), Sawant (2006), Faiz *et al.* (2006), Sharma *et al.* (2005), Swamy *et al.* (2003).
Number of panicle per plant	Veeresha *et al.* (2013b)	Akarsh and Pathak (2008), Haripresanna *et al.* (2006), Pradhan (2006), Umakanta (2002).	Zhao (2008), Sing (2005), Sawant (2006), Faiz *et al.* (2006), Sharma *et al.* (2005), Rahimi (2010).
Panicle weight	Umakanta (2002)	Haripresanna *et al.* (2006), Pradhan (2006), Shanthi *et al.*(2003)	Sharma *et al.* (2005), Zhao (2008), Sing (2005), Sawant (2006), Faiz *et al.* (2006), Rahimi (2010).
Panicle length	Veeresha *et al.* (2013b)	Swamy *et al.* (2003), Haripresanna *et al.* (2006), Pradhan (2006), Shanthi *et al.*(2003), Umakanta (2002), Vani and Rani (2003), Predeep Kumar and Reddy (2011).	Sharma *et al.* (2005), Zhao (2008), Singh (2005), Sawant (2006).
Total no of spikelets per panicle	Vani and Rani (2003),	Narasimman *et al.* (2007)	Swamy *et al.* (2003),
Spikelet fertility	Vani and Rani (2003), Swamy *et al.* (2003).	Nadali Bagheri *et al* (2010), Predeep Kumar and Reddy CVCM (2011).	
Grain yield per plant	Vani and Rani (2003), Senguttuvel and Kannan (2007), Panwan (2005),	Akarsh and Pathak (2008), Haripresanna *et al.* (2006), Pradhan (2006), Umakanta (2002), Predeep Kumarv and Reddy CVCM (2011), Shanthi *et al.*(2003), Vanaja *et al.* (2003)	Sharma *et al.* (2005), Zhao (2008), Sing (2005), Swamy *et al.* (2003), Panwan (2005), Faiz *et al.* (2006), Sawnt (2006), Rahimi (2010), Swamy *et al.* (2003), Veeresha *et al.* (2013b)
1000 grain weight	Vanaja *et al.* (2003), Senguttuvel and Kannan (2007).	Predeep Kumarv and Reddy (2011), Vani and Rani (2003), Akarsh and Pathak (2008), Haripresanna *et al.* (2006), Pradhan (2006), Umakanta (2002).	Sharma *et al.* (2005), Zhao (2008), Singh (2005), Panwan (2005), Sawant (2006), Rahimi (2010).
Number of grains /panicle	Veni and Rani (2003).	Predeep Kumarv and Reddy (2011).	Swamy *et al.* (2003).

refers to specific combining ability (SCA). Many workers have reported the additive and non-additive gene actions some reported the both for yield and productivity traits in rice as shown in Table 3.

Conclusion

The knowledge of gene action is very useful to a plant breeder in the selection of parents for hybridization. From these studies it is clear that in all these experiments GCA as well as SCA variances were found to be significant. In most cases SCA variance was reported higher than GCA variance. Further non-additive genetic variances were found higher in magnitude than corresponding additive variance for grain yield and most of the contributing characters in majority of the experiments. However equal importance of both additive and non-additive genetic components is also evident from several experiments as is the case in line x tester experiment. For the characters showing preponderance of non-additive gene action hybridization can be a choice for developing hybrids with better quantity of these traits. Simple selection has been suggested for the improvement of the characters which are mainly governed by additive gene action. The cross combinations involving poor x poor, good x good and poor x good general combining parents with highest significant SCA effects may be obtained for different traits. Crosses having both the parents as poor general combiners may involve dominance x dominance or epistatic interaction. Such crosses may not give good transgressive segregants in later generation. The crosses involving good x good general combiners and showing high SCA effects could be utilized for the purpose of developing high yielding genotypes and obtaining transgressive segregants in F_2 generation.

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