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Combining Ability and Gene Action Studies for Yield and Component Traits in Pearl Millet (*Pennisetum glaucum* (L.) R. Br.)

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ABSTRACT

The present review with respect to Combining Ability and Gene Action in Pearl millet accessing yield and component traits at individual as well as over environments revealed that both general and specific combining ability (GCA and SCA) variances were important but the estimates of Specific Combining Ability (SCA) variance was higher in magnitude than General Combining Ability (GCA) for all the characters as indicated by (GCA:SCA) ratio. Thus, indicating the predominance of non-additive gene action in the inheritance of these traits. The investigation was carried out with the object to study the general and specific combining ability variance and effects and genetic components of variation.

Keywords: Combining ability, Gene action, Yield and component traits, Pearl millet

INTRODUCTION

Pearl millet (*Pennisetum glaucum*) belonging to family Poaceae is major crop of semi-arid tropics possessing tetraploid (2n=4x=28) chromosomes. Millions of the world's poorest people of under developed countries and semi-arid tropics of Africa and Asia rely on Pearl millet for their survival. The very hardy nature of this crop has made it more acceptable to farmers of the drought prone areas, because under natural resource constraints especially rainfall, where addition of fertilizer is considered risky; pearl millet may yield higher in short duration than other cereals both with and without fertilizer applications. It has been used as a staple food for human beings and cattle since prehistoric times. Its stems and leaves have been used as fodder for cattle. The grain is chiefly used as flour for making chapattis, beverages, porridge and desserts [1-4].

India is the largest producer of pearl millet, both in terms of area (9.1 mhac) and production (7.3 m), with an average productivity of 780 kg/hac during the last five years [3]. It is a monocotyledonous and cross-pollinated annual C4 crop species. Its protogynous nature of flowering can be used to make hybrids. Choice of suitable parents is of paramount importance since per se performance of parents is not always a true indicator of its combining ability in hybrid combination [5]. 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. The combining ability analysis gives an indication of the variance due to GCA and SCA which represents a relative measure of additive and non-additive gene actions respectively [6]. Breeders use these variance components to measure the gene action and to assess the genetic potentialities of parent in hybrid combinations. Diallele [7,8] and *line × tester* [9] matting designs provide reliable information about the general and specific combining ability (GCA and SCA) of parents and their cross combinations and are helpful in estimating various types of gene actions within affordable resources. Here we are taking a review of work done by different worker all around the world for accessing the gene action, general and specific combining ability in pearl millet at individual as-well-as over environments.

The principal aim of any breeding programme is to increase the yield potential of the crop. The yield is a complex character comprising of a number of components each of which is generally polygenetically controlled and susceptible to environmental fluctuations. Under such circumstances the

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goal can only be achieved successfully by using appropriate biometrical approaches. For this intensive hybridization involving genetically diverse parents from distant sources is the most important step for releasing an array of variability. For launching this programme the selection of suitable parents with a view to incorporate desirable gene combinations in their optimum intensities is the prerequisite. The success of such breeding programme largely depends on genetic enrichment of population either through direct improvement of characters or indirect effect through component characters based on sound genetic information [1-4,10].

For the study of inheritance of yield and its components, the knowledge of the type and magnitude of gene action involved in the expression of a character is essential. Hence the present investigation; comprised of four lines and nine testers; was designed to estimate the genetics of yield and its components through the studies of genetic variability, heritability and genetic advance, combining ability analysis, heterosis and association analysis. Such studies are helpful in identification of suitable genotypes for hybrid breeding programme.

In the present review emphasis is given on Genetic Studies of Quantitative Traits in Pearl millet keeping the object to study the magnitude of genetic variability, general and specific combining ability variance and effects and genetic components of variation.

The study comprised of four male sterile lines viz., ICMA 93222, ICMA 95333, ICMA 96111, ICMA 97333 and nine inbreds used as testers viz., GIB 1, GIB 77, GIB 78, GIB 129, GIB 135, GIB 144, GIB 157, GIB 8436 and GIB 3346, of genetically diverse origin were crossed in line x tester fashion. The observations recorded on ten competitive plants in respect of combining ability studies revealed that both general and specific combining ability variance were important but the estimates of SCA. Variance was higher in magnitude for all the characters as indicated by (GCA):(SCA) ratio. Thus, indicating the predominance of non-additive gene action. General combining ability effects suggested that GIB 144, ICMA 93222, GIB 3346 and ICMA 95333 were found to be the best general combiners for yield and some of its attributes. GIB 144 showed maximum GCA effects for yield and harvest index, hence was considered most desirable. ICMA 93222 was fond to be good general combines for grain yield while GIB 3346 proved to be good general combiner for yield. Similarly ICMA 95333 was identified as good general per plant as also identified as good general combiner for yield [3,4].

COMBINING ABILITY

Sprague and Tatum [11] introduced the concept of combining ability which is the capacity of a genotype (individual) to transmit superior performance to its crosses (offspring). It is the phenomenon with which inbred lines when crossed give rise to hybrid vigor and is of two types- General Combining Ability (GCA) and Specific Combining Ability (SCA).

General combining ability (GCA)

GCA is the relative ability of a genotype to transmit desirable performance to its crosses. It is the average performance of a strain in a series of crosses, a measure of additive gene action [6].

Specific combining ability (SCA)

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, a measure of non-additive gene action [6].

Additive gene action

Additive Gene Action is the joint effect of additive variance plus additive × additive type of epistasis [6].

Non-additive gene action

Non-additive Gene Action is the joint effect of dominance and additive × dominance and dominance × dominance [6].

COMBINING ABILITY ANALYSIS

According to Singh [3] combining ability analysis provides means of understanding the nature of gene-action and helps in developing suitable breeding procedures. It has been studied extensively in cross-pollinated crops to assess the breeding value of parental lines or inbreds in terms of their superiority in hybrid combinations, and in self-pollinated crops to assess the nicking ability of varieties. The analysis is also helpful in choosing parents for hybridization programme.

Major procedure utilized in estimating the general and specific combining ability in various crop plants include (a) the diallele analysis, (b) the partial diallele technique, (c) *line* × *tester* analysis, (d) full sib and half sib analysis.

The *line* × *tester* analysis

Kempthorne [9] advanced the method of line x tester analysis which was analogous to North Carolina Design-II. He defined the general and specific combining ability variances (GCA and SCA) in terms of covariance of half sibs (H.S.) and full sibs (F.S.) in random mating population, *i.e.*,

$$\sigma 2g.c.a.=Cov.\ (H.S.)$$

$$\sigma 2s.c.a.=Cov.\ (F.S.) - 2\ Cov.\ (H.S.)$$

Though, the *line* × *tester* design offers less precise information as combining ability variance than diallele. It enjoys a few practical advantages over diallele crosses, such as the possibility of testing more parents and utilization in non-hermaphroditic species.

Certain researchers reported the utility of *line* × *tester* design in deciding about the relative capacity of number of (male and female) parents to produce desirable hybrids.

The *line* × *tester* design has the following advantages over diallele:

(a) It does not require same number of female and male parents, such that number of crosses is reduced to n × m, while diallele takes n × n number of crosses.

(b) Male and female parents are invariably different in *line* × *tester* design, whereas same parents are used both as male and female in diallele.

Combining ability in pearl millet (Studies showing both GCA and SCA effects on yield and yield components)

Researchers from their study on combining ability in pearl millet, *line* × *tester* analysis revealed that both g.c.a. and s.c.a. variances are significant for downy mildew resistance. Non-additive gene action is predominant for downy mildew, days to flower, number of tillers, plant height, ear-girth and 250-grain weight.

Yadav et al. [12] from *line* × *tester* analysis in pearl millet, under two different environments, estimated the components of g.c.a. and s.c.a. variances, showed the predominance of non-additive gene effect for all the characters except for 500-grain weight and plant height under both the environments.

Singh et al. [13] from their studies on combining ability analysis, involving 3 male sterile lines with 16 pollinators over three environments, found that both g.c.a. and s.c.a. variances were significant for grain yield, days to ear emergence, effective tillers, plant height and ear-length, over different environments. Predominance of non-additive gene effect was observed for all the characters.

Tyagi et al. [14] from *line* × *tester* analysis, involving 49 entries (36 F1s, 12 parents and one control BJ-104) of *Pennisetum typhoides* found that magnitude of variance due to females is consistently higher than due to males or *males × females*. The variance due to specific combining ability was higher than that of general combining ability in all the environments, suggesting the preponderance of non-additive gene action in controlling this character.

Mathur and Mathur [15] from their studies on combining ability in pearl millet, *line* × *tester* analysis involving 30 male parents and 5 male sterile lines, suggested that both general and specific combining ability were important in expression of all the characters but the magnitude of non-additive component was greater than that of additive component for all the characters. Therefore, it is suggested that a breeding strategy which exploits both additive and non-additive gene effects would be most effective for improving the yield.

Dass et al. [16] further carried out the studies on line x tester analysis, involving 6 male sterile lines and 10 inbred lines of *Pennisetum typhoides* reported that non-additive gene effects were predominant for all characters except for 500-grain weight. Four good general combiners and three superior crosses for grain yield were identified.

Shinde and Desale [17] from their studies on combining ability for grain yield and its components in pearl millet, *line × tester* analysis involving 4 male sterile lines and 10 inbred lines to produce 40 F1 hybrids, observed that both g.c.a. and s.c.a. effects were significant and desirable for parents and hybrids, respectively, for grain yield per plant and other yield related characters.

Singh et al. [18] from a *line* × *tester* study involving 17 inbreds and 3 testers revealed that additive variance was more important than non-additive variance for most of the traits including grain weight per plot. It was also found that the contribution to g.c.a. of the male parent was greater than that of the female when cytoplasmic male sterile lines were used.

Pethani and Kapoor [19] from their studies on combining ability and genotype × environment interaction for dry fodder yield in pearl millet involving *line* × *tester* analysis found both additive and non-additive gene effects were important. However, later have a slight edge over the former. But the additive component was more stable. High specific combining ability effects in hybrids were reflected due to additive and epistatic gene interaction.

Kunjir and Patil [20] through their study on *line* × *tester* analysis for combining ability in pearl millet, involving 4 male sterile lines and 10 inbreds revealed that: (1) general combining ability (g.c.a.) estimates for female parents were higher than the specific combining ability (s.c.a.) estimates for most yield components indicating the predominance of additive effects; and (2) s.c.a. effects were more important than g.c.a. effects for grain yield per plant indicating the predominance of non-additive effects. Lines with good g.c.a. and crosses with good s.c.a. were also indicated.

Pathak and Ahmad [21] found that the additive component appeared predominant for most of the characters studied except tiller synchrony and smut incidence.

Srivastava and Singh [22] observed that significant differences among parents and hybrids for grain yield and harvest index. Good g.c.a was shown by GIB1 for days to maturity, MS81, MS834, GIB1, GIB144 and GIB3/DMR for grain yield and MS842, GIB 144 and GIB Violet for harvest index.

Srivastava and Singh [22] studied ear-length and diameter and test weight in a diallele cross of 10 genetically diverse *Pennisetum americanum* inbreds. Both g.c.a and s.c.a variances were significant for ear-length and test weight whereas only g.c.a variance was significant for ear diameter.

Ahuja et al. [23] studied grain yield, harvest index and 3 yield-related characters in a 10 × 10 diallele cross of *P. typhoides* (*P. americanum*) inbreds. Variance due to g.c.a and s.c.a was significant for all characters. Moderate heritability was recorded for harvest index and effective tillers/plant while grain yield and biological yield showed poor heritability.

Navale et al. [24] reported that additive gene action is important for grain yield, days to 50% flowering and production of tillers and s.c.a effects revealed the importance of dominant gene action for ear-length and plant height.

Some suggested that grain yield was largely governed by non-additive gene action but was accompanied by some significant additive gene action. General combining ability variance due to the female plants (male-sterile lines 5054-A, 5141-A, L111-A and 126D2A) was significant whereas that due to the male component was non-significant under all environments. Distortions in the proportions of s.c.a. and g.c.a. variances were attributed to a strong genotype × environment interaction.

Setty and Appadurai [25] reported that the nature of gene action was predominantly additive for panicle length, whereas dominance gene effects were important for the remaining characters.

Gill et al. [26] reported that the variances due to g.c.a were non-significant, while variances due to s.c.a. were significant for all the qualitative traits studied, indicating preponderance of non-additive gene action in the control of the inheritance of quality traits.

Chavan and Nerka [27] observed that g.c.a. variance attributable to male parents were much larger than any other component. Specific combining ability (s.c.a.) variance was predominant for all characters, indicating the importance of non-additive gene effects.

Some researchers observed that both additive and dominance type variance existed for all the characters under study in the synthetic population RBS2.

Kandaswami and Ramalingam [28] evaluated nine cytoplasmic male-sterile lines of pearl millet and six inbreds for combining ability for 6 yield related characters in a line x tester mating design. Analysis of g.c.a. and s.c.a. variances indicated the importance of non-additive effects for days to 50% flowering, panicle-girth and grain yield per plant.

Pethani and Kapoor [29] found that both non-additive and additive genetic variances played an important role. However, former was more important for days to ear emergence and plant height, whereas later for grain weight. For all the characters both the components interacted with the environments. However, non-additive genetic variance was found more responsive to environmental changes. Complementary type epistasis was responsible for crosses having high desirable s.c.a. effects. Per se performance and g.c.a. effects of parents were related for days to flowering and plant height. The s.c.a. effects and mean performance of hybrids were not related for these characters.

Aher and Ugale [30] reported that in both the generations the mean sum of squares for general and specific combining ability indicated the role of additive as well as non-additive gene effects for the expression of these characters. However, non-additive gene effects were predominant for all characters except ear-head girth in the F1.

Naik et al. [31] evaluated forty hybrids of *Pennisetum typhoides* (*P. glaucum*) for combining ability. The analysis of variance revealed significant differences between parents for ear-length, plant height, days to 50% flowering and maturity. The estimates of combining ability variances suggested the predominance of non-additive gene action in the control of all the yield contributing characters studied.

Devanand and Das [32] showed the predominance of general combining ability (g.c.a.) variance over specific combining ability (s.c.a.) variance for days to 50% flowering, internode length, green fodder yield, dry matter yield and crude protein and oxalate contents, indicating the preponderance of additive gene action. The predominance of non-additive gene action was recorded for plant height, number of tillers, leaf area, stem girth, number of leaves and calcium content as these showed higher s.c.a. variance than g.c.a. variance.

Azhaguvel and Jayaraman [33] reported predominance of non-additive gene action for all the characters in the study.

Karale et al. [34] obtained that non-additive genetic variance predominantly governed the expression of yield, 1000 grain weight, productive tillers/plant and leaves/main shoot. Additive gene action was important for days to 50% flowering, plant height, ear length, ear-girth and grains per cm^2.

Latha and Shanmugasundaram [35] indicated that non-additive gene action was found predominant for all the characters except ear length, where additive type of gene action was noticed.

Mohan et al. [36] derived information on heterosis, combining ability and genetic variance from 30 progeny of a 5 line × 6 tester pearl millet (*Pennisetum glacum*) cross. The results indicated that additive gene action was important for number of productive tillers, ear-head length, ear-head girth and 1000-grain weight.

Mitra et al. [37] reported that additive component was predominant for number of leaves per plant, leaf breadth and stem diameter whereas dominance genetic variance was significant for plant height and ratio of leaf-to-stem. However, number of tillers per plant, leaf length, dry fodder yield and green fodder yield per plant showed significance for both additive and dominance components.

Yadav et al. [38] evaluated the combining ability of 7 newly developed male sterile lines and 11 testers of forage pearl millet. Variance due to lines, testers and their combinations was significant for all traits tested. The s.c.a. estimates were higher for dry fodder yield and effective tillers, indicating the preponderance of non-additive gene effects for these traits. For plant height, the additive component was high, as indicated by the predictability ratio.

Lakshamana et al. [39] studied combining ability for grain yield and yield components in forty F1 hybrids and their parents. The estimates of general combining ability (g.c.a.) revealed significant variation among the parents for plant height, ear-length, number of days to maturity and number of days to 50% flowering. The estimates of combining ability variances suggested the predominance of non-additive gene effects for most of the yield components.

Rasal and Patil [40] reported the involvement of non-additive gene action for grain yield per plant and additive gene action for plant height, days to flower, tillers per plant, ear-girth and ear-length was observed.

Researchers conducted a *line × tester* analysis, using eight male sterile lines and eight restorer lines, on yield and some component traits in pearl millet. The results revealed that the mean sum of squares due to general and specific combining ability were significant, suggesting the importance of both additive and non-additive components.

Rathore et al. [41] conducted an experiment on pearl millet to study the combining ability of 11 diverse restorer lines by diallel mating design. Variances due to both s.c.a. and g.c.a. were significant for all the characters except s.c.a. for panicle-girth, indicating importance of both additive and non-additive gene action.

Shanmuganathan et al. [42] crossed 11 diverse pearl millet genotypes in a diallele mating system and noted that the variance due to g.c.a. and s.c.a. were significant. For all characters except leaf breadth, g.c.a. variances were higher in magnitude than s.c.a. variances, indicating the preponderance of additive gene action. For leaf breadth, both g.c.a. and s.c.a. variances were equal, indicating the prevalence of both additive and non-additive gene action.

Sushir et al. [43] crossed seven male sterile lines and 10 restorers and evaluated the resulting 70 hybrids and 17 parents to understand the combining ability and nature and magnitude of gene action in pearl millet. The general combining ability effects were higher than the s.c.a. effects for number of productive tillers per plant and ear-length, indicating the role of additive gene action in the expression of these characters whereas it was the reverse for days to 50% flowering, ear-girth and grain yield per plant.

Bhanderi et al. [44] studied combining ability in 8 × 8 diallele set, for grain yield and its 12 attributes in pearl millet. Both g.c.a. and s.c.a. variances were highly significant for all characters. The predictability ratio of g.c.a. and s.c.a. revealed preponderance of additive genetic variance for plant height, ear-head length, ear-head girth and 1000-grain weight whereas non-additive genetic variance for days to 50% flowering, days to maturity, number of effective tillers per plant, fodder yield per plant, harvest index and grain yield per plant, while, both were equally important for number of nodes, ear-head weight and threshing index.

Kumhar and Singhania [45] indicated significant differences among genotypes for all the characters on pooled as well as in individual environments. Mean sum of squares due to parents vs. hybrids were significant for all the characters indicating presence of heterosis. The estimates of g.c.a. and s.c.a. variances were significant for most of the characters in both the environments indicating the importance of both additive and non-additive gene actions in the inheritance.

In a 10 × 10 half diallel excluding reciprocals Dangariya et al. [46] evaluated the combing ability and gene action involved in respect of yield and its attributes in pearl millet. Analysis of variance indicated highly significant differences among mean squares due to general and specific combining ability for all the characters studied.

Chotaliya et al. [47] carried out combining ability analysis in a 10 × 10 diallele set excluding reciprocals, for yield and 11 yield components in pearl millet. The present study revealed the importance of non-additive gene action in the inheritance of traits viz., grain yield per plant, fodder yield per plant, 1000-grain weight and harvest index, while additive gene action was preponderant for plant height, ear-head length, ear-head girth and ear-head weight. Both additive and non-additive gene action were found in days to 50% flowering, days to maturity, number of effective tillers/plant and number of nodes.

Dar et al. [6] concluded from their studies that in all GCA as well as SCA variances were found significant and 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. The researchers also found some correspondence between good general combiners and per se performance for some of the traits.

In their studies, Bhadalia et al. [48], Shinde and Mehetre [49], Nandaniya et al. [50], Kumar et al. [10], reported cross with high SCA effects involving good × good general combiners for grain yield per plant and related traits. These crosses offer good promise for improvement of respective component traits and ultimately grain yield. The transgressive segregants could be isolated in higher frequency from these cross and utilize to generate inbreds lines using conventional breeding methods for further crop improvement programmes.

Singh and Sharma [4] evaluated the combing ability of 4 male sterile lines and 9 testers of pearl millet in line x tester fashion. Analysis of s.c.a. effects revealed that good combining parents yield better hybrids, because parents with significant positive g.c.a. effects were involved more in selected crosses than those with non-significant g.c.a. effects and negative g.c.a. effects. In the present study, the involvement of at least one good general combiner was found essential for obtaining combinations with high specific effects. Combining ability studies revealed that both general and specific combining ability variances were important but the estimates of s.c.a. variance were higher in magnitude for all the characters. Thus, indicating the predominance of non-additive gene action.

IMPLICATIONS IN FUTURE BREEDING PROGRAMME

From the present review it appeared that combining ability analysis provides powerful tools in the hands of plant breeder in selection of suitable parents with a view to incorporate desirable gene combination in their optimum intensities. Results of combining ability analysis revealed that GIB 144, ICMA 93222, GIB 3346 and ICMA 95333 were the best general combiners for yield and its attributes, hence may be used as parents in future hybridization programme for the improvement of yield. Seven crosses viz., ICMA 93222 × GIB78, ICMA 96111 × GIB129, ICMA 93222 × GIB 144, ICMA 93222 × GIB 129, ICMA 97333 × GIB 157, ICMA 97333 × GIB 135 and ICMA 95333 × GIB 157 exhibited high SCA effects for most of the yield contributing characters. Thus, these are isolated as best specific combiners for yield and its components [3,4].

A breeding methodology that can exploit both additive- and non-additive genetic effects would be the most effective in attaining maximum improvement in yield and its components characters in pearl millet. The importance of SCA effects for characters like grain and effective tillers per plant may depend on material studied and due to high genotype × environment interaction. Generally the high divergence of parents contributes to high SCA effects. Such cross combinations may further be exploited for the isolation of broad based widely adopted varieties through population-breeding approach in the form of bi-parental mating between selected recombinants as well as mating of selected segregants between crosses in early segregating generations. Recommendations may be brought in the light of manipulations of yield contributing traits in order to tailor a suitable plant type that may give better yield [3,4].

The combining ability studies revealed that both general and specific combining ability variance were important but the estimates of SCA variance were higher in magnitude than GCA variance for all the characters, thus indicating the predominance of non-additive type of gene action. These findings are in close agreement with the findings reported by Singh et al. [13], Tyagi et al. [14], Mathur and Mathur [15] and Pethani and Kapoor [19]. But Chavan and Nerker [27] noted much larger GCA variance for male parents.

Conflicting views have been reported in the literature regarding the relative importance of general vs. specific combining ability for various quantitative traits. It was found that s.c.a. variance was higher in magnitude for grain yield while reverse was the case for yield components. Similar results were reported by Kunjir and Patil [20]. Moreover, some have also reported high GCA effects as compared to SCA effects for ear-length and ear-girth. Apart from this scientists noted more SCA than GCA for tillering to the above results. Singh et al. [18] and Navale et al. [24] revealed that additive variance was more important than non-additive variance for most of the traits including grain weight per plot. However, researchers noted the presence of both GCA and SCA variance for grain yield, ear-length and ear-girth, while Singh et al. [1], Shinde and Desale [17], Mathur and Mathur [15], Dass et al. [16] suggested that both GCA and SCA variances were important in expression of all the characters. Pathani and Kapoor [19] further suggested the importance of both additive and non-additive gene effects but found additive component was more stable. High SCA effects in hybrids were due to additive and epistatic gene interaction.

The data from the hybrid trials were further analyzed to determine the GCA (male and female) and SCA (male × female interaction) variance component for each character. Variance due to SCA of females was found consistently high as compared to variance due to GCA of males for all the characters. The estimates of GCA and SCA variances and their ratio further reaffirmed the preponderance of non-additive gene effects for all the characters.

COMBINING ABILITY EFFECTS

General combining ability effects

The results obtained in the present investigation have indicated that none of the parent exhibited high GCA effects for all the characters under study.

Among the male parents, GIB 144 proved to be the best general combiner as it showed maximum GCA effects for yield. It also showed second highest GCA effects for ear-length.

However, GIB 3346 was identified as good combiner for stem thick-ness, leaf area, flag leaf length, grain yield per plant and dry weight per plant.

Among the female parents, ICMA 93222 was found to be good general combiner for number of productive tillers, grain density and dry weight per plant, whereas ICMA

95333 proved to be good general combiner as it showed significant GCA effects for stem thickness, leaf area, flag leaf length, panicle length, grain yield per plant and dry weight per plant.

It was quite evident from the above results that the parents showing high GCA effects for grain yield (GIB 144, ICMA 93222, GIB 3346) also showed high GCA effects for other yield components. GIB144 was one of the best combiners for grain yield. It also showed high GCA effects for other components. Griffing [7] suggested that yield is an end product of multiplicative interactions between yield components. It was found that all high combiner for yield were also high combiner for one or more of the other yield components **(Table 1)**.

Table 1. The best general combiners showing high g.c.a. effects for different traits.

S. No.	Characters	Best General Combiners		
		I	II	III
1.	Plant height	ICMA 97333	GIB 1	GIB 135
2.	Stem thickness	GIB 144	GIB 3346	ICMA 95333
3.	Leaf area	GIB 144	ICMA 95333	GIB 3346
4.	Flag leaf length	ICMA 95333	GIB 3346	--
5.	No. of productive tillers/plant	GIB 1	ICMA 93222	--
6.	Panicle length	GIB 77	GIB 144	GIB 129
7.	Panicle-girth	GIB 144	ICMA 97333	--
8.	Grain density	GIB 135	GIB 129	ICMA 93222
9.	1000-grain weight	GIB 144	ICMA 97333	GIB 8436
10.	Grain yield per plant	GIB 144	ICMA 93222	GIB 3346
11.	Dry weight per plant	GIB 144	ICMA 93222	ICMA 95333
12.	Harvest index	GIB 144	GIB 8436	ICMA 96111

None of the parents showed significant positive GCA effects for number of nodes per main stem and number of leaves per main stem.

Similar was the case with ICMA 93222. It was found to be good general combiner for yield and also showed high GCA effects. Thus, indicating that high GCA effects were related to high GCA effects for yield. Researchers also reported that high GCA effects were related for yield. Some had also obtained similar results for different characters in pearl millet.

Parent ICMA 97333 was found to be good general combiner for plant height, panicle-girth, 1000-grain weight but it showed negative GCA effects for yield. Hence it was not considered desirable for further breeding programmes. Similarly GIB 1 was identified as good general combiner showed poor results for yield. In such cases SCA effects should be considered for combining these characters with yield.

General combining ability (GCA) effects of the parents revealed that GIB 144, ICMA 93222, GIB 3346 and ICMA 95333 were good general combiners for yield and yield contributing components. All these parents could be inter-mated to develop a base population with new recombinants. Base population thus developed could then be improved by appropriate method of recurrent selection such as S2 and S1 progeny selection system, full sib selection system and combine half sib and S1 selection system. Elite population thus developed may serve as the source material for use in developing superior hybrid combination, synthetic and experimental varieties.

Specific combining ability effects

The specific combining ability estimates revealed that no cross combination was consistently superior for all the characters under study as reported by various researchers.

Seven crosses viz., ICMA 93222 × GIB 78, ICMA 96111 × GIB 129, ICMA 93222 × GIB 144, ICMA 93222 × GIB 129, ICMA 97333 × GIB 157, ICMA 97333 × GIB 135 and ICMA 95333 × GIB 157 were identified as the best specific combiners for yield and major yield components.

For better comparison as sample of seven best crosses, selected on the basis of high SCA effects for yield and its components in order of merit have been listed in **Table 2**.

Table 2. Best specific cross combination for yield and its components.

Crosses	s.c.a. effects for yield per plant	s.c.a. effects for yield components in desirable direction
ICMA 93222 × GIB 78	High	2, 3, 4, 7, 13, 14
ICMA 96111 × GIB 129	High	2, 5, 8, 9, 11, 13
ICMA 93222 × GIB 144	Medium	2, 3, 4, 10, 13
ICMA 93222 × GIB 129	Medium	3, 4,7, 10, 13
ICMA 97333 × GIB 157	Medium	7, 11, 13
ICMA 97333 × GIB 135	Medium	1, 7, 11, 14
ICMA 95333 × GIB 157	Medium	2, 5, 6, 8, 9, 11, 13

Where, 1=Plant height; 2=Stem thickness; 3=Number of nodes per main stem; 4=Number of leaves per main stem; 5=Leaf area; 6=Flag leaf length; 7=Number of productive tillers per plant; 8=Panicle length; 9=Panicle girth; 10=Grain density; 11=1000-grain weight; 12=Grain yield per plant; 13=Dry weight per plant; 14=Harvest index

As indicated in the **Table 2**, the cross combination ICMA 93222 × GIB 78 was identified as best cross as it showed high SCA effects for yield as well as for other characters. While the cross combination ICMA 96111 × GIB 129 was considered second best for yield, it also showed positive SCA effects.

Apart from this the hybrid ICMA 93222 × GIB 144 showed significant positive SCA for yield whereas the hybrid ICMA 93222 × GIB 129 also exerted the SCA effects in positive direction for both yield and its components, similarly the cross combination ICMA 97333 × GIB 157 showed SCA effects in positive direction for yield.

The other two hybrids also showed significant positive SCA effects for yield as well as for other yield components. Hybrid ICMA 97333 × GIB 135 showed SCA effects while the hybrid ICMA 95333 × GIB 157 showed positive SCA effects.

Analysis of SCA effects revealed that, in general, good combining parents (with significant GCA effects) yield better hybrids, because parents with significant positive GCA effects (high) were involved more in selected crosses than those with non-significant GCA effects (medium) and negative GCA effects (low). The crosses from high × high, high × medium and high × low have given better specific combinations due to the presence of genetic diversity in the form of heterozygous loci for specific traits. In the present study, the involvement of at least one good general combiner was found essential for obtaining combinations with high specific effects. For example, in the case of hybrid ICMA 93222 × GIB 78, parent ICMA 93222 was a good general combiner for most of the characters while parent GIB 78 was a low combiner, whereas in the hybrid ICMA 93222 × GIB 144 both the parents were high combiners. Several workers, Mathur and Mathur [15] and Dass et al. [16] have also made similar observations in pearl millet. However others noted that low combiners may also give high specific combining ability effects.

Certain researchers emphasized that the superiority of the mean of hybrids might not elucidate their ability to produce transgressive segregants due to non-fixable portion, specific combining ability in segregating generation, therefore would be important under such circumstances. In order to select best specific combination which is likely to result in desirable transgressive segregants in segregating generation, it is useful to select such derivatives which are stable in both F1 and F2 generations.

Recurrent selection is a breeding system having some theoretical superiority over the standard system of continuous self-pollination. In view of this it may be desirable to treat the advanced generations of the crosses which have shown high SCA for grain yield as separate population and to use them in recurrent selection programme. Reciprocal recurrent selection could be followed to exploit additive as well as non-additive effects as indicated by Mathur and Mathur [15].

The utilization of combining ability studies for hybrid breeding programme is of great value since the production of male sterile lines and restorer lines is a laborious and time consuming procedure. Hence, it is worthwhile having information on choice of parent early in the programme. According to some researchers, g.c.a. is important in previously unselected material while SCA assumes importance in material previously selected for GCA They suggested that for hybrid sorghum production the parents should be selected on the basis of GCA effects of parents, SCA effects of crosses which are likely to result in transgreasive-segregants in segregating generation [51,52].

CONCLUSION

From the present study it appeared that combining ability analysis provides powerful tools in the hands of plant breeder in selection of suitable parents with a view to incorporate desirable gene combination in their optimum intensities. Results of combining ability analysis revealed that GIB 144, ICMA 93222, GIB 3346 and ICMA 95333 were the best general combiners for yield and its attributes, hence may be used as parents in future hybridization programmes for the improvement of yield.

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