

Review

Combining ability and gene action studies for important horticultural traits in chilli, *Capsicum annuum* L

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ABSTRACT

Identification of hereditarily superior parents has always been pre-requisite in chilli for the improvement of best strains. The combining ability analysis is the basic, most important and efficient tool in selecting the desirable parents for breeding programme. It is based on first degree statistics which is statistically robust. It helps in estimation of inbreds in terms of their genetic value and in the selection of best parents for hybridization in chilli. Further it also helps in identification of superior cross combinations which may be utilized for exploitation of heterosis commercially. Gene action helps in selection of appropriate breeding procedures for improvement of various characters thereby necessitating breeders to initiate a judicious breeding programme in chilli. Therefore combining ability and gene action analysis have been the most important and efficient tool in selecting the desirable parents for a hybridization, selection of breeding procedure and estimation of genetic parameters. This review will be more helpful in understanding the opportunities offered by combining ability and gene action studies in chilli.

Keywords: Combining ability; gene action; chilli; horticultural traits; *Capsicum*

INTRODUCTION

Chilli, *Capsicum annuum* L belong to family Solanaceae consumed either in a green or as dried red ripe fruit throughout the world for its pungency in culinary preparations or as pickles. It is generally preferred in fresh, dried or processed items and is the most extensively used high value

spice in India. India is a leading producer of chilli and has a great diversity within the country. It is a self-pollinated crop but on an average 15-16 per cent natural crossing has also been noted in it (Ram 1998). It occupies an important place in Indian diet and is consumed daily as a condiment in one form or the other. The pungency in chilli is due to principle component capsaicin

contained in the pericarp and placenta of fruits. India contributes about 36 per cent to the total world production of the crop (Karpate and Saxena 2010).

The origin of cultivated *C. annuum* is South America. It is herb sometimes subshrub due to woody base, erect and tap root grown as annual. The main shoot is radial but lateral branches are cincinnate one of the branches at each node remaining underdeveloped and subtending bract or bracts are adnate and carried up a lateral shoot to node above (Rai and Yadav 2005). Leaves are simple; flowers are borne singly and terminal and sometimes appear axillary due to form of branching.

Identification of genetically superior parents for the development of elite strains is an important prerequisite. The combining ability analysis is the most important and efficient tool in choosing the desirable parents for hybridization programmes (Sharma et al 2013). The concept of combining ability was enunciated by Sprague and Tatum (1942). They partitioned the genetic variances into two components viz variance due to general combining ability (GCA) and variance due to specific combining ability (SCA). The GCA is defined as the average performance of lines/strains in a set of cross combinations and the SCA as those instances in which certain cross combinations do relatively better or worse than would be expected on the basis of average performance of the

parental lines involved crops combination. It is also expressed that GCA is mainly the result of additive gene effects and additive $\times$ additive interactions while SCA is consequences of dominance, epistatic deviation and genotype $\times$ environmental interactions. This also reveals that in cases where the estimates of SCA variance (σ^2 SCA) were large than those of GCA variance (σ^2 GCA) the importance of epistatic and dominance effects are more than the additive gene effects.

Griffing (1956a) reported that the GCA includes both additive effect as well as additive $\times$ additive interactions. The high yielding lines may not necessarily be able to transmit their superiority to their hybrids (Allard 1960). Hayman (1957) presented the work on the nature of gene action and heterosis in diallel set of crosses in maize, cotton and tobacco. He observed that in the absence of epistasis GCA comprised of both additive and dominance portion of variance while SCA involved mainly dominance portion of variance. However when epistasis is present the estimates of both GCA and SCA contain epistatic portion and observed that SCA was mainly a measure of dominance and epistasis in unselected and selected materials respectively.

With the progress of biometrical genetics several techniques have been evolved for the estimation of combining ability (Sharma et al 2013). Of these top

cross proposed by Davis (1927) and elaborated by Jenkins and Brunson (1932), poly cross technique suggested by Tysdal et al (1942), diallel cross analysis by Griffing (1956b), line $\times$ tester analysis by Kempthorne (1957), partial diallel cross by Kempthorne and Curnow (1961) and triallele cross by Rawlings and Cockerham (1962) are used to estimate combining ability. The hybridization program of crop breeding envisages the recombination and variability in crop plants. The magnitude of these genetic effects is influenced by the nature of gene action comprising number of genes controlling the character, degree of dominance and inter-allelic effects of the traits (Sharma et al 2013). Thus the aim of this review is to provide a basic knowledge of breeding which will be useful for traditional breeders, horticulturists and other plant scientists as well as students. It helps in analyzing the information of component of variance which is involved in the expression of various quantitative characters and selection of desirable parents for hybridization.

Combining ability and gene action

Combining ability

Gopalkrishnan et al (1987) investigated and hybridized between four chilli lines, Jwala, Pant C-1, CA 33 and CA 23 in a half diallel to estimate heterosis and combining ability. Involvement of both additive and non-additive gene actions was detected for the control of plant height,

primary branches/plant, leaf laminar length, fruit length and days to flower. Out of six hybrids four exhibited significant relative heterosis for plant height and one for fruit length. Taking into consideration the per se performance heterosis and SCA effect Jwala $\times$ Plant C-1 was the best hybrid yielding 201 g/plant followed by Jwala $\times$ CA 23 (160g/plant). All the hybrids were earlier than the mid-parents of which three were even earlier than the early parents.

Bhagyalakshmi et al (1991) estimated heterosis and combining ability in six chilli varieties (LCA 206, LCA 1079, LCA 960, LIC 13, X-235 and G 4) by crossing in a half diallel. Involvement of both additive and non-additive gene actions was detected for days to 50 per cent flowering, days from fruit set to fruit maturity, fruit length, fruit girth, fruits/plant, fresh fruit weight, 100-dry fruit weight and 100-seed weight with greater predominance of non-additive gene action. Taking into consideration the per se performance SCA effects and heterosis LCA 206 $\times$ LCA 960 was the best hybrid yielding 638.3 g/plant followed by LCA 206 $\times$ LA 1079 (535.2 g/plant). The varieties LCA 960, LCA 206 and G 4 were the best general combiners for majority of the characters which gave high GCA effects for yield/plant with positive and significant GCA effects for many of the yield characters. Out of the 13 characters studied the manifestation of heterosis over mid-parent was maximum (upto 160.3%) for number of branches/plant.

Shukla et al (1999) concluded that non-additive gene effect was found to be responsible for the expression of all the traits except fruit length and girth for these two traits and additive gene effect was important. Parents Jwala × Jagudan 103 were good general combiners for green fruit yield and other important yield contributing components. About 1/3 hybrids depicted significant SCA effect for green fruit yield.

Lohithaswa et al (2000) evaluated ten parents and their 45 F₁s of chillies from a half diallel cross for fruit yield and its components over three environments. Highly significant variation was observed due to genotypes and environments for ten traits studied. The genotype × environment interaction was significant for all the characters except days to initiation of flowering. The genotypes Pant C-1, Arka lohit, RHRC 16-5 and X-235 were found to be good general combiners and 15 crosses have been identified as specific combiners for fruit yield and other related traits.

Patel et al (2001) studied that all the characters except number of fruits per plant were largely influenced by specific combining ability variance; average degree of dominance revealed that those were predominating controlled by additive genes effect. The parents ACS 97-1, ACS 98-9, Be 14-2, Punjab Guchhedar and RHRC-16-S were identified as good

general combiners for green fruit yield and important yield contributing component characters. The hybrids ACS 97-1 x SG-5, ACS-97-1 x Resham Patti and ACS 98-9 x Balochpur depicted significant SCA effects for green fruit yield and other yield contributing attributes along with higher estimates of heterobeltiosis.

Singh and Hundal (2001) crossed three female and fourteen male parents in line x tester fashion for studying combining ability analysis for oleoresin and related characters in chilli. Non-additive components predominated for dry matter, colouring matter in powder and oleoresin, oleoresin (%) and oleoresin yield while additive components predominated for capsaicin in powder and oleoresin. The female parent Punjab Guchhedar was good combiner for dry matter, capsaicin in powder and oleoresin, oleoresin (%) and oleoresin yield. The male parent Punjab Lal was good combiner for dry matter, capsaicin in powder and oleoresin, S-2529 for oleoresin, colouring matter in powder and oleoresin. The cross combinations M5-12 × 5-2530, Lt-2 × RHCH Up, Punjab Guchhedar × S-2545 and Punjab Guchhedur × LLS recorded significant SCA effect for oleoresin yield, oleoresin (%), capsaicin in powder and colouring matter in powder respectively.

Srivastava et al (2004) selected six genetically diverse lines/varieties of chilli namely PC-1, Iwala, 339, 7722, 8601 and

Raj-1 from the germplasm available at Vegetable Research Station, Kalyanpur of CS Azad University of Agriculture and Technology, Kanpur for making diallel cross to study the combining ability during 1996-97. During 1997-98 15 F_1 s and their six parents were studied in RBD with three replications. Results indicated that parents namely Pant C-1, 339 and 7722 were best general combiners for yield, earliness and pod character. The hybrids 8601 $\times$ 7722, PC-1 $\times$ 339 and 8601 $\times$ Raj-1 were best specific crosses for several characters on the basis of specific combining ability effect. The results suggested exploitation of hybrid vigour in chilli.

Jagadeesha and Wali (2005) studied on eighteen divergent lines of chilli and 45 F_1 hybrids to investigate the general and specific combining ability effects for five yield components. Higher proportion of additive gene effect was noticed for all the characters. The parents Byadagi Kaddi, VN-2, Arka Lohith, KDC-1, LCA-312 and Jwala were identified as good general combiners for dry fruit yield and important yield contributing characters. The hybrids B-Kaddi $\times$ KDC-1, VN-2 $\times$ BC-24, VN-2 $\times$ LCA-301, B-Kaddi $\times$ LCA-301 and B-Dabbi $\times$ Arka Lohith depicted significant SCA effects for dry fruit yield and other yield contributing attributes. The pedigree selections are suggested for exploitation of additive gene action in some crosses. Heterosis breeding is suitable to produce new hybrid combination for increasing the fruit yield.

Geleta et al (2006) assessed twenty one F_1 hybrids and seven parental genotypes for combining ability and heritability for vitamin C and total soluble solids in pepper (*C. annuum* L). The mean squares for general (GCA) and specific (SCA) combining abilities were highly significant for the two traits suggesting the importance of both additive and non-additive gene effects. However additive gene action was more important as GCA estimates were much higher than SCA effects. Among the parental genotypes Mareko Shote, PBC 142A and PBC 142A were good general combiners for vitamin C and total soluble solids respectively and could be used to improve these traits in pepper breeding programmes for the accumulation of favourable genes. They also showed the highest per se performance (315.3 mg 100/g and 18.5°Brix respectively) for the two quality traits. The narrow sense heritability estimate for vitamin C was relatively high (54.8%) indicating that the environment had a less pronounced effect on this trait. The heritability for total soluble solids was low (15%).

Prasanth and Ponnuswami (2008) evaluated six diverse genotypes Arka Lohit, MDU Y, S1, Arka Abir, Bydagi Kaddi and Co 4 for general and specific combining ability, variance components and standard heterosis. Among the lines Bydagi Kaddi, MDUY and Arka Abir were found to be good general combiners for yield and quality characters. The estimates of GCA

and SCA variance for all the characters except for leaf area index, dry yield per hectare and capsaicin suggested preponderance of additive gene action than non-additive. The cross combination MDU Y $\times$ Co 4 had desirable significant SCA effects for yield and quality characters namely fresh yield, dry yield, total extractable colour and capsaicin. The estimates of heterosis over best parent ranged from 40.35 to 126.32 per cent for the character dry yield per hectare. In the study based on per se performance, heterosis and SCA effects the hybrids Bydagi Kaddi $\times$ Arka Abir and MDU Y $\times$ Co 4 were found superior in respect of total extractable colour, low capsaicin besides dry yield and contributing characters.

Rego et al (2009) estimated the general and specific combining ability of peppers by measuring fruit quality and yield traits. This experiment was carried out on the garden field from Universidade Federal de Viçosa (UFV), Minas Gerais State-Brazil. Eight lines of *C. baccatum* belonging to the UFV Horticultural Germplasm Bank were chosen based on their broad genetic and phenotypical background variation and were crossed in a complete diallel way. The F_1 seed of the 56 hybrids and eight parents were planted in the field in a randomized complete block design. The data were submitted to ANOVA and the means were grouped by Scott-Knott test ($P \leq 0.01$). Significant variation for fruit quality and yield components was observed among parents

and F_1 generation. Analysis of variance for the combining ability showed that GCA effects exhibited significant difference and SCA effects of the crosses were significant except for the height of first bifurcation. For almost all characters both additive and non-additive effects influenced the performance of hybrids.

Gene action

Manju and Sreelathakumary (2002) studied thirty two accessions of hot chilli (*C. chinense* Jacq) to estimate the variability, heritability and genetic advance in randomized block design with three replications. Higher phenotypic and genotypic coefficients of variation were observed for fruits per plant, yield per plant, seeds per fruit and fruit weight. High estimates of heritability coupled with high genetic advance were also observed for these characters.

Sreelathakumary and Rajamony (2004) investigated thirty five chilli (*C. annuum* L) genotypes to assess genetic variability, heritability and genetic advance. Higher phenotypic and genotypic coefficients of variation were observed for leaf area, fruits per plant, fruit weight, fruit length, fruit girth and yield per plant. High heritability coupled with high genetic advance observed for these characters imply the potential for crop improvement through selection. High heritability combined with high genetic advance could be regarded as an indication of additive gene

action and the consequent high expected genetic gain from selection for these characters.

Blat et al (2006) studied on powdery mildew and its reaction inheritance in chilli. Two powdery mildew resistant parents Pimenta Cheiro 1 and PI 152225 and two moderately susceptible ones Pimenta Doce IH-1761 and Pimenta Índio were used to obtain three F_1 and their respective F_2 generations: Pimenta Doce IH-1761 $\times$ Pimenta Cheiro 1, Pimenta Índio $\times$ PI 152225 and Pimenta Doce IH-1761 $\times$ PI 152225. The powdery mildew epidemic was natural using inoculum from a highly sporulating susceptible pepper host. Powdery mildew host reaction evaluations were carried out during the fruiting stage using a rating system based on disease severity scales varying from 1 (resistant) to 5 (highly susceptible). The experimental design was completely randomized. The following genetic parameters were estimated: gene action, heritability coefficient and expected selection gain in the F_3 generation. The transgressive segregation in F_2 indicated oligogenic inheritance. Results showed the presence of additive, dominant and epistatic gene action. The dominant and epistatic effects detected in crosses presented negative values tending towards susceptibility. The heritability and selection gain estimates were moderate with values of 35.5 and 1.7 per cent for Pimenta Doce IH 1761 $\times$ Pimenta Cheiro 1, from 50.4

to 3.5 per cent for Pimenta Índio $\times$ PI 152225 and 49 and 2.7 per cent for the Pimenta Doce IH 1761 $\times$ PI 152225 crosses respectively. These gene action results are favorable for breeding programs and exploration of hybrids.

Singh and Yadav (2008) evaluated thirty six genotypes (8 parents of diverse origin and their 28 F_1 s excluding reciprocals) to estimate their genetic variability, heritability and genetic advance. Most of the characters were observed with wide range of variability. In the present investigation high to moderate heritability with high to moderate genetic advance were observed for number of seeds per fruit, ascorbic acid content, number of fruits per plant, fresh fruit weight per plant, fresh fruit yield (q/ha), seed weight per plant and seed yield (q/ha) showing dominance of additive gene effects which suggested excellent chance of effective selection for improvement of these traits and high heritability coupled with medium genetic advance for stem diameter and total soluble solids and suggesting good chances of effective selection for these traits. While other traits showed non-additive type of gene action.

Somashekhar and Salimath (2008) carried out to unravel the nature and magnitude of gene effects in VN-2 $\times$ Jwala, VN-2 $\times$ Arka Lohit, Hissar Shakti $\times$ PMR-21, Byadagi Kaddi $\times$ Arka Lohit and Byadagi Dabbi $\times$ LCA-312 crosses for

quantitative characters in chilli through generation mean analysis. For VN-2 x Arka Lohit, Byadagi Kaddi x Arka Lohit and Byadagi Dabbi x LCA-312 crosses higher magnitude of dominance gene effect was observed as compared to additive gene effect while additive x additive 'i' component was more predominant than other types of interactions. Although the dominance gene effects were predominant it cannot be exploited because of the opposite signs of 'h' and 'i' gene effects in all the crosses except Dabbi x LCA 312 (9623) cross. Whenever these gene effects ('h' and 'i') co-existed it indicates the presence of duplicate epistasis.

Murmu et al (2014) conducted an experiment at Central Research Farm, Gayeshpur, Bidhan Chandra Krishi Viswavidyalaya, Nadia, West Bengal where moderate GCV coupled with high broad sense heritability and moderately high genetic advance was registered in three characters namely fruit yield/plant, number of fruits /plants, fruit girth and seeds/fruit. So simple selection should also be rewarding in terms of improving these characters. Very low heritability accompanied with very low to moderately low genetic advance was recorded for fruit length, fruit weight, pericarp thickness and pedicel: fruit ratio indicating less responsiveness of these characters to selection. Improvement of these characters needs selection over several successive years preferably across locations and over

different plantings because such association of genetic parameters may be attributed to non-additive gene action. From the results of genetic variability fruit yield/plant, number of fruits/plant, fruit girth and seeds/fruit emerged as most reliable characters for selection because of their probable conditioning by the additive gene action.

Singh et al (2009) investigated thirty genotypes of chilli pepper (*C. annuum* L) during the summer rainy seasons of 2005 and 2006 to study the extent of genetic variability, determine the association between different characters, understand direct and indirect effects of component traits on fresh and dry yield and identify desirable genotypes. Sufficient variability was observed for all horticultural and quality traits studied viz days to 50 per cent flowering, days to first harvest, primary structural branches per plant, secondary branches per plant, fruit length, fruit diameter, average fruit weight, number of seeds per fruit, 100-seed weight, pericarp: seed ratio, number of marketable fruits per plant, number of total fruits per plant, plant height, marketable yield per plant, total soluble solids and oleoresin, capsanthin and capsaicin content. High phenotypic (PCV) and genotypic coefficients of variation (GCV) were observed for marketable fresh and dry yield per plant, number of marketable fruit, average fresh and dry fruit weight, fruit length and diameter, seed weight per fruit, number of primary structural branches per plant and oleoresin

and capsaicin content. Moderate PCV and GCV were recorded for number of secondary branches per plant, plant height, harvest duration, number of seeds per fruit, 100-seed weight, pericarp: seed ratio, ascorbic acid, and capsanthin. High heritability coupled with high genetic advance was noted for marketable fresh and dry yield per plant, average fruit weight, numbers of marketable fruit, fruit diameter and oleoresin and capsaicin content which indicated the role of additive gene action for the inheritance of these traits.

Chattopadhyay et al (2011) conducted an experiment to identify the most promising chilli variety suited for green and dry purposes to study the genetic variability for different traits and to assess the association of different yield attributing traits with the green and dry yield of chilli. Thirty four genotypes were characterized during a 2 year period. Most of the genotypes possessed the character constellation of *C. annuum*. Two genotypes Chaitali Pointed and BC CH Sel-4 were found most promising with respect to green fruit yield (272.79 g, 221.10 g per plant) and dry fruit yield (54.56 g, 44.44 g per plant). Phenotypic and genotypic coefficient of variation values for green fruit weight (119.95%, 111.26%), green fruit girth (89.76%, 48.93%), weight of red ripe fruit (112.02%, 111.93%), weight of dry fruit (111.63%, 110.97%) and number of fruits per plant (86.05%, 85.02%) were recorded to be high. Green fruit yield per plant, ascorbic acid content and number of fruits

per plant also showed very high broad sense heritability and genetic advance. The genetic advance (GA) which is expressed as a percentage of mean was very high for characters like green fruit yield per plant (122.97), ascorbic acid content (102.60) and number of fruits per plant (74.75) which had high value of broad sense heritability indicating a preponderance of additive gene action for the control of these traits.

Dhamayanthi and Reddy (2011) transferred two agronomically desirable characters from CA-33 and CA-219 to two popular chilli cultivars G-4 and CO-2. The F_1 hybrids and their segregating population F_2 , BC_1 and BC_2 were raised to determine the gene action in respect of the fruit orientation and clustered fruit character. The results revealed that genes responsible for the clustered fruit character were monogenic while the upright fruit character was digenic controlled by two genes with dominant and recessive epistasis.

Hasanuzzaman and Golam (2011) studied on gene action for yield and yield contributing traits in four selected crosses of chilli (*C. annuum* L) involving five parents including their F_1 s, F_2 s and first back cross generations. The significant scaling tests (one or more scales in A, B and C) and joint scaling test indicated the presence of digenic epistasis for all the studied traits. Number of fruits and yield per plant were controlled by additive, dominance and epistatic gene action. Complex genetic behavior was observed in all traits. Since

the segregating generations did not follow a simple Mendelian inheritance high selection pressure is expected in later generations due to probable successful exploitation of additive and dominance components. From these observations it is suggested that the selection for the improvement of all traits particularly yield per plant should be delayed to the later generations of segregating population in this plant. The modified bulk method of selection is recommended in which selection is performed after attaining the homozygosity for maximum heterozygous loci. Presence of complementary gene action and prevalence of the high magnitude of non-additive gene effects were found in most of the traits indicating that heterosis breeding is more effective with high potential in chili.

Pandit and Adhikary (2014) evaluated forty one chilli genotypes which were grown in a randomized block design with three replications during autumn-winter season of 2010-11 at the AB block Farm, Kalyani, Bidhan Chandra Krishi Viswavidyalaya, Nadia, West Bengal to estimate variability and heritability for important reproductive and yield characters. In the experiment genotypic coefficient of variation and phenotypic coefficient of variation estimates closely corresponded with regard to days to 50 per cent flowering, fruit length, placenta length and 1000-seed weight; in others it differed moderately altogether suggesting low to medium influence of environment in

the expression of these characters. Close estimates of phenotypic coefficient of variation and genotypic coefficient of variation were noted in all characters except fruit width which imply that contribution towards final phenotypic expression of these characters are mostly genetic rather than environmental. Very high genetic advance as per cent of mean was recorded in fruit yield/plant and moderately high genetic advance as per cent of mean was recorded in days to 50 per cent flowering, placenta length, fruit length, number of fruits/plant and number of seeds/plant indicating that these characters are most likely governed by additive gene action and hence would be rewarding in selection.

CONCLUSION

The concept of gene action is much useful to breeder for the selection of parents in hybridization programme to estimate the genetic parameters and choice of breeding procedures for the genetic improvement of various quantitative characters. In a self-pollinated crop exploitation of non-additive genetic variance as such would be impossible. Since the literature exhibited that earliness and yield attributing traits were predominantly controlled by additive gene effects simple selection method like single seed descent would be effective for isolating short duration progenies in advanced generations. The cross combinations involving $P_1 \times P_1$, $P_2 \times P_2$ and $P_1 \times P_2$ general combining parents with highest

significant SCA effects may be obtained for different horticultural traits. Crosses having both the parents as low general combining ability may involve dominance x dominance or epistatic interactions. Such crosses may not give good transgressive segregants in further generations. The crosses involving high (P_1) x high (P_1) general combiners and showing high SCA effects could be utilized for developing high yielding genotypes.

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