

Review

Combining ability and gene action studies for horticultural traits in garden pea: A review

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Identification of genetically superior parents is an important prerequisite in garden pea for the development of elite strains. The combining ability analysis has been the most important and efficient tool in choosing the desirable parents for hybridization programmes. The attraction of combining ability is that this provides an empirical summary of complex observations and a reasonable basis for forecasting the performance of yet untested crosses but yet makes no assumptions genetically. Being based on first degree statistics (totals, means), they are statistically robust and, being genetically, so to speak, neutral, they are equally applicable to in breeder and out breeder, whether seed propagated or clonal. This technique 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 characters. 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 be help in understanding of the exciting opportunities offered by combining ability and gene action studies in graden pea (*Pisum sativum var. hortense* L.).

Key words: Combining ability, garden pea, gene action, horticultural traits.

INTRODUCTION

Garden pea (*Pisum sativum var. hortense* L.), belongs to leguminosae family, is one of the most popular vegetable crop grown all over the world, both for fresh market and the food processing industry. It has a prominent place among vegetables due to its high nutritive value, particularly proteins and other health building substances like carbohydrates vitamin A, vitamin C, calcium and phosphorus (Sharma, 2010). It is grown commercially as a winter crop in the northern Indian plains and as a summer crops in the high hills. It is one of the most popular off season vegetable crop grown in north-western Himalaya region in India. For the development of elite

strains, the identification of genetically superior parents is an important prerequisite. The combining ability analysis is the most important and efficient tool in choosing the desirable parents for hybridization programmes. The concept of combining ability was enunciated by Sprague and Tatum (1942). They partitioned the genetic variances into two components (i) variance due to general combining ability (GCA) and (ii) 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

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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 revealed 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) suggested 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). Hence, an estimate of GCA and SCA effects may be a more reliable test than the *per se* performance of the lines. 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 advancement of biometrical genetics, several techniques have been evolved for the estimation of combining ability. Of these, top cross proposed by Davis (1927) and elaborated by Jenkins and Brunaon (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 system of plant 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. Our review has been specifically written for readers with only a basic knowledge of plant breeding. It will be a useful reference for conventional plant breeders, horticulturist and other plant scientists, as well as students. It will be of help in understanding the exciting opportunities offered by combining ability and gene action studies. This review has been reviewed under the following sub heads.

COMBINING ABILITY AND GENE ACTION

Combining ability

Singh et al. (1972) evaluated the progeny of a 5 \times 5 diallel set excluding reciprocals for yield and it is of the

contributing traits. They reported that both GCA and SCA variances were significant for all the traits. It reflected the importance of additive and non-additive gene actions. The GCA effects were prominent in characters such as plant height, pod length and pod width, where as in number of pods per plant and number of seeds per pods, SCA affects were pronounced in the material. Das and Kumar (1975) observed that both GCA and SCA variances were predominant for yield, number of branches, number of pods and seeds per pod, while SCA variances were higher for seed yield per plant. Gritton (1975) crossed eight cultivars of pea in diallel and the parents; F_1 's and F_2 's were evaluated for 2 years at two locations in Wisconsin and reported both general and specific combining ability were important for days to flowering, plant height, pods per plant, seed per pod, seed per plant and seed yield. Venkateswarlu and Singh (1981) conducted field trial with 10 \times 10 diallel analysis in pea and the parents; F_1 's and F_2 's were evaluated for five quantitative characters. They found that both general and specific combining ability were important for plant height, primary branches, pods/plant, 100-seed weight and seed yield/plant. The mean squares from diallel analysis of the F_1 crosses showed that the variances due to both GCA and SCA were highly significant for all the character studied.

Singh et al. (1986) derived information from a 10 \times 10 diallel analysis and reported that the genotypes BR-12 and EC-33866 were found good general combiners for protein content. Srivastava et al. (1986) studied combining ability and heterosis in an eight parents half diallel cross analysis in pea and found both general and specific combining ability mean squares significant for all the traits studied. Considering together GCA effects for all the 11 traits, it appeared that Rachna, P-29 and P-185 were the best general combiners followed by HFP-4 and Dola. In general, a positive relationship was recorded between SCA effects and estimates of heterosis. It was observed that the best general combiners were also best specific combiners. Gupta and Lodhi (1988) evaluated nine cultivars of garden pea in a half-diallel analysis for days to pod formation and days to maturity. Parents EC-109189, T-163, EC-09196 and P-23 were found good general combiners for days to pod formation and days to maturity. Cross combinations EC -109189 \times T-163, EC-109189 \times P-23, EC-109189 \times EC-109196, T-163 \times EC-109196 and T-163 \times P-23 showed significant negative SCA effects and thus, were promising for selecting early genotypes. Singh and Singh (1989) studied genetics of earliness in terms of flower initiation and days to maturity in F_1 of 12 parents in a diallel cross in pea. Mean squares due to both GCA and SCA were highly significant, suggesting the importance of both additive and non-additive genetic variance controlling these characters. The parents EC-33866, A-474-228, GC-322 and Sel-2 were good general combiners with negative GCA effects for early flowering and maturity. The *per se* performance

parents was observed to be positively associated with their GCA effects. The SCA effects for early flowering in EC-33866 × ED followed by Sel-2 × T163 in F_1 were the best cross combinations.

Karmakar and Singh (1990) observed in a 5 × 5 diallel experiment that JP-169 was the best general combiner for yield and its components followed by VP-7802. The genotype VP-8005 was good general combiner for seeds per pod and Arkel for dwarf stature. Glorisa × JP 169 was the best specific combination for yield and yield component characters followed by Arkel × VP-7802 and JP 169 × VP 8005. Arkel × VP 8005. The cross combination was the promising combination for seeds per pod. Chung and Chang (1992) studied combining ability of major agronomic characters in pea and their F_1 hybrids grown over three years in field. 'Alderman' was most promising parent based on general combining ability effects.

Kumar and Bal (1995) studied inheritance of economic traits a set of eight cultivars of garden pea. Bonneville was observed as the best general combiner. The cross combinations Wando × P-35, Arkel × P-35, Hara Bonna × GC-141, Arkel × GC-141 and Arkel × GC-141 were the best specific combiners for pods per plant, pod length, number of seeds per pod, hundred seed weight and yield per plant respectively. Panda et al. (1996) were found parents PH-1, HUVP-1, EC-33866 and VL-6 to be good general combiners for green pod yield, number of seeds per pod, days to first picking of green pods and the cross combination HUVP-1 × EC-33866 was reported the best specific combination for total green pod yield per plant. Singh and Mishra (1996) studied heterosis and combining ability in 6 × 6 diallel set of mid season peas and found cultivar Bonneville was the best general combiner followed by VP-7906. The estimates of SCA effects showed that cross Bonneville × JP-169 performed best for pod length, pod width and grains per pod. However, 10 out of 15 cross combinations (VP-7906 × C-152 being highest) showed negative SCA for days to 50% flowering, which tends towards the earliness. In most of the cases, SCA variances were found to be higher than those of GCA variances for early maturity. Bhardwaj and Kohli (1998) found that the parents VL-3, Lincoln, Kinnauri, Ageta-6 and Arkel were good general combiners for yield and yield traits. They had observed that the crosses showing high estimates of SCA effects usually did not involve both the parents having high GCA effects. Most of the crosses showing significant and positive SCA effects involved high × low general combiners.

Narayan et al. (1998) studied combining ability from data derived on pod yield and three quality components viz., dry matter content, total soluble solids and protein content and six yield components in pea varieties and their 15 F_1 cross combinations. The cultivar Bonneville was the best combiner for all the quality traits. Sharma (1999) observed that the parents Azad P-1, Palam Priya

and VL-7 were the best general combiners, while cross combination VL-7 × DPP-13 showed significant and positive SCA effects for all 5 yield components except grains per pod. Sharma et al. (2000) carried out combining ability analysis from diallel cross of pea cultivars and found that GCA variance were significant for all characters except pod breadth for which SCA variance was higher. The *per se* performance of parents and crosses was usually associated with the combining ability effects. Singh et al. (2001) derived information on combining ability in garden pea involving twenty one crosses and seven parents. The GCA and SCA variances were highly significant for all the traits (days to flowering, days to maturity, plant height, number of primary branches per plant, number of pods per plant and pod length). The SCA variances were predominant in comparisons to GCA variances for all the characters that indicated the greater contribution of non-additive gene action in the expression of these characters. Kumar and Jain (2002) conducted field trial with 8 × 8 diallel analysis in garden pea and observed that variety Arka Ajeet showed highest GCA effects for characters including number of pods per plant and plant height. The cultivar had revealed Bonneville higher GCA for earliness, number of pods per plant and pod yield per plant. Cross combination Arka Ajeet × Bonneville had revealed highest SCA for pod yield per plant and number of pods per plant followed by PMR- 20 × KS-136.

Singh and Mishra (2002) derived information on combining ability in 10 × 10 diallel set. The mean sum of squares due to GCA and SCA variances were highly significant for all the characters except seeds per pod. The parents PDP-52 and Azad P-1 were the best general combiners for seed yield per plant. Three cross combinations PDP-23 × PDP-52 in F_1 and PDP-33 × PDP-55 and PDP-41 × PDP-55 in F_2 had exhibited desirable significant SCA effects for four characters. Dixit (2003) reported that the cross combinations IPF × KPMR and IPF- 98-9 × MS NDP-90-1 showed significant and desirable SCA effects as well as high *per se performance* for pod yield per plant and number of pods per plant. The cross combination IPF-98-9 × NDP-90-1 showed significant SCA effects and good performance for plant height. Singh and Singh (2003) evaluated F_1 and F_2 generations of pea in a 10 × 10 diallel set of crosses. The magnitude of SCA effects was recorded higher than GCA effects for all the traits under investigation except days to first flowering and days to maturity.

Zaman and Hazarika (2005) derived information on general and specific combining ability effects. Parent Rachna and HUP-2 were found to be good general combiners for green pod yield and most of the other characters. Azad pea was good general combiner for earliness. The cross combinations Rachna × Azad pea, Rachna × HUDP-6 and Azad pea × HUP-2 exhibited higher and significant SCA effects for yield and majority of the characters. Ranjan et al. (2005) conducted field

trial involving 7 × 7 diallel mating design excluding reciprocals for yield and its components. Parents KPMR-327, KPMR-228, NDP-93 were observed as good general combiner and crosses HUP-15 × KPMR-327, KPMR-327 × LFP-179 as superior cross combinations for yield contributing characters. Pandey et al. (2006) reported that combining ability analysis showed significant difference for GCA and SCA variance for all the characters. Parent Lincoln appeared to be one of the best combiners for all the traits including plant height in desired direction. On the basis of combining ability studies general combiners for plant height (dwarfness, UD-1, Lincoln), pods per plant (Pahari Matar, NC-64086), pod length (Lincoln, J-4), seeds per pod (Lincoln, UP-7839), pods yield per plant (Lincoln, NC-64086) and Arkel UD-1 for total soluble solids were identified. Sood et al. (2006) reported that the varieties Palam Priya and JI-2334 of garden pea the best parent for protein content. Bonneville proved to be the best combiner for pod yield per plant, shelling percentage, dry matter content, and protein content, whereas Lincoln and VL-3 were the best combiners for all the traits except shelling percentage and protein content. These parents also produced some crosses with high SCA effects for more than one trait. Bonneville × Lincoln exhibited positive significant SCA effects for all the characters except dry matter content, while as Solan Nirog × Kiannauri recorded significant and positive SCA effects for all traits except pod yield per plant (Raj, 2006). The prevalence of additive and non-additive gene action in the inheritance of yield and quality traits suggested that the suitability of recurrent selection in succeeding generations for the development of transgressive segregants.

Singh et al. (2007) conducted a field study with 10 × 10 diallel analysis (without reciprocals) in edible podded pea. The mean squares for general combining ability were observed higher than those of specific combining ability in all the characters. Variety Sugar Bon showed highest GCA for days to 50% flowering and number of branches per plant and the second highest GCA for plant height. Variety Mithiphali was recorded with highest GCA effects for total and marketable green pod yield per plant. Cross combination Sugar Daddy × JP-19 recorded highest specific combining ability for total and marketable green pod yield per plant followed by Early Snap × Mithiphali. Sharma et al. (2007) carried out a line × tester analysis involving 10 promising lines and 2 testers having wider genetic base for pod yield and related horticultural traits in garden pea at diverse environments at Kukumseri (dry-temperate) and Palampur (sub-temperate) during summer 2004 and winter 2004 and 2005, respectively. Among the parents, Green Pearl, Azad P 1, DPP 9418-06 and DPP 9411 were observed as good general combiners for pod yield/plant and majority of the component traits. The cross combinations Green Pearl × DPP 9411 and Azad P 1 × Sugar Giant showed high heterosis and SCA effects for pod yield and related

horticultural traits. The cross Green Pearl × Sugar Giant was the most promising for early flowering and green pod picking. For powdery mildew incidence, the cross VRPMR 10 × Sugar Giant where both parents revealed high negative GCA effects also showed significant negative SCA effect and heterosis. For most of the traits including pod yield/plant, both additive and non-additive gene actions were of prime importance.

Kalia and Sood (2009) evaluated F1's and F2 progenies of eight divergent parents mated in diallel fashion excluding reciprocals for combining ability in green pea for the horticultural characters. However, the SCA variance component was predominant indicating the importance of non-additive gene effects for all the characters except for peas per pod and pod yield which were influenced by additive gene action, suggesting their improvement through pure line selection. Palam Priya was found to be the best general combiner for all traits and is thus the most suited as parent for improving productivity and other desirable traits in garden pea. To ensure further increase in pod yield along with high protein content, cross combinations involving desirable yield components is advocated, with JI 1559 × Matar Ageta 6 as the best combination. To further improve pod yield, inclusion of F1 combinations with high SCA and parents with good GCA in multiple crosses, biparental mating, or diallel selective mating could be a worthwhile approach.

Singh et al. (2010) observed higher values of variance due to GCA for days to flowering, days to maturity, plant height, pod length, number of developed ovules per pod, shelling percentage and green pod yield per plant showed presence of additive gene action while it was non additive for number of productive branches per plant and number of pods per plant based on both the generations. Parents 'KS-226', 'KS-225', 'KS-136', 'Azad P-1 and 'Azad P-3' were good general combiners for green pod yield based on both the generations. The average performance of table pea parents was better than field pea parents. Cross combinations namely 'KPMR-184 × KS-136', 'Rachna × KS-225', 'KS-195 × AP-3', 'KPMR-184 × Mutant pea' and 'Mutant × KS-136' in F1, 'KS-195 × KS-225', 'KPMR-184 × AP-3', 'Mutant × KS-226', 'KS-226 × AP-1' and 'KPMR-65 × KS-226' in F2 were found as good specific combinations for green pod yield. The majority of these crosses falls in the high × low general combiners. The crosses between table × field pea gave higher yield than table × table or field × field pea.

Sirohi and Singh (2013) reported lines HPPC 41, HPPC 77, HPPC 91 and HPPC 94 for leaf area and total chlorophyll content and HPPC 60, HPPC 67 and HPPC 84 for specific leaf weight were good general combiners. While HPPC 67 × HPPC 63, HPPC 69 × Lincoln, and HPPC 94 × Lincoln were the promising crosses for specific leaf weight, chlorophyll-a and chlorophyll-b contents, respectively, on the basis of specific combining ability.

Gene action

Genes are the functional units that govern the development of various characters of an individual. Gene action refers to the behaviour or mode of expression of genes in a genetic population. Genes control synthesis of proteins which in turn control expression of various traits of organisms. Knowledge of gene action in plant breeding helps in the selection of parents for use in the hybridization programmes and also in the choice of appropriate breeding procedure for the genetics improvement of various quantitative characters. Klence insight into the nature of gene action involved in the expression of various quantitative characters is essential to a plant breeder for starting a judicious breeding programme.

Narsinghani et al. (1982) reported that additive genetic variance in pea was significant for seed yield per plant, while epistatic gene action was positive for number of pods and seeds per plant. There was a positive additive, dominance and over dominance gene action for seeds per plant. The monogenic system for days to flowering was observed by Ram et al. (1981) in peas, but non-additive gene action was noted by Singh et al. (1986).

Singh et al. (1986) derived information from a 10×10 diallel analysis and reported that non-additive gene action was predominant for protein content. The persistence of SCA component for protein component indicated that additive \times additive component was predominant. Mean degree of dominance indicated over dominance for protein content. Negative correlation coefficient (r) between parental order of dominance ($W_r + V_r$) and parental measurement (Y_r) for protein content indicated that the dominant alleles contributed positively for the expression of this trait. Regression coefficient for protein content significantly different from unity, suggesting the presence of non-allelic interaction of genes. The regression line passed below the origin, suggesting over dominance for protein content. Rastogi et al. (1989) found significant non-additive components in case of protein content in pea seed. Singh and Singh (1987) derived information in diallel analysis for combining ability in pea. The estimates for GCA and SCA variance indicated that both additive as well as non-additive genetic components were involved in determining the inheritance of these traits. Srivastava and Singh (1988) found both additive and non-additive gene effects to be important in genetics of seeds per pod in peas but non-additive gene effects were more prevalent than additive effects. Gupta and Lodhi (1988) evaluated nine cultivars of garden pea in a half diallel analysis for days to pod formation and days to maturity and observed the preponderance of both additive as well as non-additive gene effects for both traits. The complete dominance was observed for days to pod formation and over-dominance for days to maturity. The ratio of K_D/K_R (Ratio of dominant allele and recessive allele) revealed excess of dominance

alleles for both the traits. Symmetry of distribution of positive and negative genes in the parents was indicated only for days to maturity as the estimates of $H_2/4H_1$ were close to 0.25. Positive correlation of Y_r and ($W_r + V_r$) for days to pod formation showed importance of recessive alleles favouring delaying of pod formation, while negative association for days to maturity indicated importance of dominant alleles for late maturity. Singh and Ram (1988), observed that additive and non-additive gene action predominated for days to flower, green pods per plant, 100 green pod weight, pod length, shelling percentage, number node at which appear of first flower, primary branches per plant, plant height and green pod yield in diallel analysis of garden pea. Genetic components of variation analysis supported these conclusions. Rastogi (1988) reported the presence of high non-additive genetic variance (H_1 and H_2) as compared to additive genetic variance (D) in a diallel analysis of ten parents for vitamin C content of garden pea seed in F_1 generation, The ratio of $H_2/4H_1$ was very near to the expected value of 0.25. K_D/K_R ratio in the parents was more than 1 revealing the predominant role of dominant alleles. The SCAtter of parental arrays suggested that the parents such as GC - 66 and Bonneville contained greater number of dominant genes for higher vitamin C content. Singh and Singh (1989) studied genetics of earliness in terms of flower initiation and days to maturity in F_1 of 12 parents in a diallel cross in garden pea. The additive and non-additive components of genetic variance were significant for these characters. Karmakar and Singh (1990) observed that the analysis of variance for combining ability has revealed the role of additive as well as non-additive gene action in controlling the characters seed yield per plant, pods per plant, and seeds per plant, plant height and days to flowering. However, non-additive gene action was predominant for these characters ($\sigma^2_g/\sigma^2_s < 1$).

Rana and Gupta (1994) carried out genetic analysis of green pod yield and found that it was influenced by over dominance. Sarawat et al. (1994) found that both additive and non-additive gene effects were important in the expression of grain yield, branches per plant, pods per plant, seeds per pod, plant height and onset of flowering. Kumar and Bal (1995) carried out graphical analysis and predicted over dominance for yield, number of pods per plant, 100 seed weight and partial dominance for other. The dominance variance was higher for all the traits except pod length and seeds per pod. The degree of dominance indicated over-dominance for all the traits except pod length and seeds per pod. The distributions of genes in the parents were asymmetrical for all the variables. Sirohi et al. (1995) found that additive \times dominance and dominance \times dominance types of non-allelic interactions were important in the inheritance of traits like days to flowering, days to maturity and plant height. Singh et al. (1997) carried out genetic analysis to detect epistasis and to estimate components of genetic

variance. Significant estimates of both additive and dominance components were observed for all the traits, except for pod length. The direction of dominance (F value) was positive and significant for days to flowering, plant height, pod per plant and seed yield indicating the isodirectional nature of dominance. Raj et al. (1998) studied genetics of yield and its components in garden pea. The characters like pod yield per plant, number of seeds per pod and number of pods per plant showed either significant additive or dominance or both gene effects along with (i), (j) or (l) types of epistasis in one or more cases. Sharma et al. (1999) observed the presence of both additive and non-additive type of gene action in pea. The σ^2_A to σ^2_D ratio indicated the pre-dominant role of non-additive gene action for pod yield, pods per plant, days to pod maturity and shelling percentage, while additive gene action was found important for plant height. Singh and Sharma (2001) recorded in a diallel analysis of 8 parents for five characters that additive gene effects were significant and positive in two crosses for plant height, number of pods per plant, number of seeds and pod yield per plant. Almost all the F_1 crosses had positive dominance gene effects for plant height, number of pods per plant, number of seeds per pod, pod length and pod yield per plant and a higher magnitude than that of additive gene effects. In diallel analysis of 10 parents for earliness, Sharma et al. (2003), reported that the additive (D) and non-additive (H_1) components of genetic variance were significant for earliness. The degree of dominance was in partial dominance range in F_1 and over dominance range in F_2 . The ratio of $H_2/4H_1$ revealed the symmetrical distribution of negative and positive alleles among the different parents. The ratio of K_D/K_R was more than unity in F_1 indicated excess of dominant alleles in the expression of these traits.

Ranjan et al. (2005) found that the σ^2_g/σ^2_s ratio was estimated to determine the importance of additive and non-additive genetic variances. The variance ratio was less than unity for days to flowering, plant height, branches per plant, days to maturity, pods per plant, seeds per pod and seed yield per plant. Sood and Kalia (2006) conducted inheritance studies on seven economic traits viz., days to 50% flowering, days to first picking, pods per plant, seeds per pod, pod yield per plant and shelling percentage in a diallel set of eight parents excluding reciprocals in garden pea. From 28 F_1 crosses as well as their F_2 's prevalence of over dominance was observed for most of the traits in both the generations. Non-additive gene action appeared to be more predominant for the inheritance of most characters studied. Dominant alleles were more frequent in parental lines for the inheritance of most of the characters. Low to medium narrow sense heritability indicated presence of non-additive gene action for most of the traits except for pod yield. Dhillon et al. (2006) reported additive and non-additive gene effects governed the inheritance of all the studied characters. The additive gene effects were more

pronounced for days to flower initiation, node at which first pod appears, number of branches per plant, plant height, number of pods per plant, pod length, days to marketable maturity and shelling percentage, whereas the non-additive gene effects were more pronounced for number of seeds per pod, dry matter content and total green pod yield per plant.

Sharma and Sharma (2012) observed the prevalence of over dominance for most of the traits except for node number at which first flower appear. However, additive and dominance genetic variance were highly significant for days to 50% flowering and days to first harvest. For green pod yield per plant the regression line was linear and slope ($b = 0.2532 + 0.1734$) of regression varied significantly from unity suggesting the prevalence of non-allelic interactions. Low estimates of narrow sense heritability indicated the presence of non-additive gene action for most traits except for days to 50% and days to first harvest. These characters also exhibited medium to high level of heritability and the selections in segregating generation could be effective for evolving early maturing types.

Sharma and Bora (2013) reported higher values of heritability in broad sense and genetic gain indicating that the additive gene actions are important in determining the characters viz. plant height, days to first picking, 100 green pod weight, green pod yield and days to 50% flowering revealed. Therefore, selection programme based on these characters would be more effective in improving yield parameters of garden pea. Combining ability analysis for six physiological characters in pea revealed leaf area and chlorophyll-a/b ratio was governed by additive gene action. While both additive and non-additive gene actions were important for controlling total chlorophyll, chlorophyll-a, chlorophyll-b contents and specific leaf weight as found by Sirohi and Singh (2013).

CONCLUSION

The knowledge of gene action is very useful to a plant breeder in the selection of parents for hybridization, the estimation of some other genetic parameters and choice of breeding procedures for the genetic improvement of various quantitative characters. In an autogamous crop exploitation of non-additive genetic variance as such would be impractical. Since, the research investigation exhibited that earliness and yield attributing traits were predominantly controlled by additive gene effects, simple selection procedure like single seed descent would be effective for isolating short duration progenies in advanced generations. Simple progeny selection may be followed for selecting transgressive segregants in later generations for developing genotypes having long pods. 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 horticultural 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 F2 generation.

REFERENCES

- Allard PW (1960). Principles of Plant breeding. Wiley and Sons Publisher, New York. pp. 138-142.
- Bhardwaj RK, Kohli UK (1998). Combining ability analysis for some important yield traits in garden pea. *Crop Res. Hisar*. 15:245-249.
- Chung HJ, Chang KY (1992). Studies on the combining ability of major agronomic characters in pea. *Korean J. Crop Sci.* 37:250-256.
- Das K, Kumar H (1975). Combining ability analysis of yield and its certain components in pea. *Madras Agric. J.* 62:18-22.
- Davis RL (1927). Report of Plant breeder. Puerto Rico Agric. Exp. Sta. Ann. Rept. pp. 14-15.
- Dhillon TS, Singh M, Singh H (2006). Combining ability studies of genetically diverse lines in garden pea. *Haryana J. Hort. Sci.* 35(3/4):334-337.
- Dixit GP (2003). Combining ability analysis in Field pea. *Indian J. Pulses Res.* 16(1):20-21.
- Griffing B (1956b). Concept of general and specific combining ability in relation to diallel crossing system. *Aust. J. Biol. Sci.* 9:463-493.
- Griffing B (1956a). A generalized treatment of the use of diallel crosses, in quantitative inheritance *Heredity*. *Aust. J. Biol. Sci.* 10:31-50.
- Gritton ET (1975). Heterosis and combining ability in a diallel cross in peas. *Crop Sci.* 9:463-493.
- Gupta KR, Lodhi CP (1988). Gene effects and combining ability for earliness in pea. *Agric. Sci. Digest*. 8(1):15-18.
- Hayman BI (1957). The theory and analysis of diallel crosses-II. *Genetics* 43:63-85.
- Jenkins MT, Brunaon (1932). A method of testing inbred line of maize in cross bed combinations. *J. Ann. Sci. Agron.* 24:523-530.
- Kalia P, Sood M (2009). Combining ability in the F1 and F2 generations of a diallel cross for horticultural traits and protein content in garden pea (*Pisum sativum* L.). *SABRAO J. Breed. Genet.* 41(1):53-68.
- Karmakar PG, Singh RP (1990). Combining ability in early peas. *Veg. Sci.* 17:95-98.
- Kempthorne D, Curnow RN (1961). The partial diallel cross. *Biometrics* 17:229-240.
- Kempthorne O (1957). An Introduction of Genetics Statistics. John Wiley and Sons, New York. pp. 458-471.
- Kumar A, Jain BP (2002). Combining ability studies in pea (*Pisum sativum*). *Indian J. Hort.* 59(2):181-184.
- Kumar JC, Bal SS (1995). Inheritance of economic traits in garden pea (*Pisum sativum* L.). *Haryana J. Hort. Sci.* 24(3-4):251-255.
- Narayan R, Sharma DK, Narayan S, Kanaujia SP (1998). Studies on combining ability for quality traits in pea (*Pisum sativum* L.). *Indian J. Hill Farming*. 11(1-2): 108-110.
- Narsinghani VG, Rao USN, Singh SP (1982). Diallel cross analysis for quantitative traits in mutant pea types. *Indian J. Agric. Sci.* 52:364-367.
- Panda PK, Singh KP, Kar RM (1996). Combining ability analysis for some quantitative characters in garden pea (*Pisum sativum* L.). *Ann. Agric. Res.* 17:230-234.
- Pandey V, Pant T, Das SC (2006). Studies on heterosis and combining ability in pea. *Indian J. Hort.* 63(3):338-340.
- Raj N (2006). Combining ability for quality attributes in garden pea (*Pisum sativum* var. *hortense* L.). *Environ. Ecol.* 24(2):464-467.
- Raj N, Rastogi KB, Dogra BS (1998). Genetics of yield and its components in garden pea. *Veg. Sci.* 25:18-21.
- Ram HH, Singh RD, Singh YV (1981). Note on inheritance of resistance to powdery mildew and days to flowering in peas. *Curr. Sci.* 50:782-784.
- Rana JC, Gupta VP (1994). Genetic analysis of green pod yield and phenological traits in pea. *Legume Res.* 17:105-108.
- Ranjan S, Kumar M, Pandey SS (2005). Genetic studies in pea involving tall and dwarf genotypes. *Legume Res.* 28(3):202-205.
- Rastogi KB (1988). Genetics analysis of vitamin C content in green seed of pea (*Pisum sativum* L.). *Haryana J. Hort. Sci.* 16(3-4):241-247.
- Rastogi K.B, Sharma PP, Korla BN (1989). Genetic analysis of protein content in pea seed (*Pisum sativum* L. var *hortense*). *Veg. Sci.* 16:175-180.
- Rawlings JO, Cockerham CC (1962). Analysis of double cross hybrid populations. *Biometric* 18:229-244.
- Sarawat P, Stoddard FL, Marsall DR, Ali SM (1994). Heterosis for yield and related characters in pea. *Euphytica* 80:39-48.
- Sharma A, Singh G, Sharma S, Sood S (2007). Combining ability and heterosis for pod yield and its related horticultural traits in garden pea (*Pisum sativum* L.) under mid-hill sub-temperate and high-hill dry-temperate conditions of Himachal Pradesh. *Indian J. Genet. Plant Breed.* 67(1):47-50.
- Sharma A, Vidyasagar, Singh A (2003). Gene action and combining ability studies for earliness in garden pea (*Pisum sativum* L.). *Veg. Sci.* 30(1):83-84.
- Sharma BB (2010). Combining ability and gene action studies for earliness in garden pea (*Pisum sativum* L.). A thesis M Sc submitted to G B Pant University of agriculture and Technology Pantnagar. P. 10.
- Sharma BB, Sharma VK (2012). Genetic analysis for earliness and yield Traits in Garden pea (*Pisum sativum* L.). *Vegetos* 25(1):63-67.
- Sharma DK, Bala AC, Bala A (1999). Studies on combining ability and gene action in pea (*Pisum sativum* L.). *Indian J. Hill Farming* 12:32-36.
- Sharma MK, Rastogi KB, Korla RN (2000). Combining ability analysis for yield and yield components in pea (*Pisum sativum* L.). *Crop Res. Hisar*. 19:500-504.
- Sharma TR (1999). Combining ability and heterosis in garden pea (*Pisum sativum* var. *arvense*) in the cold desert Himalyan region. *Indian J. Agric. Sci.* 69:386-358.
- Sharma VK and Bora Lila (2013). Studies on genetic variability and heterosis in vegetable pea (*Pisum sativum* L.) under high hills condition of Uttarakhand, India. *Afr. J. Agric. Res.* 8(18):1891-1895.
- Singh D, Mishra VK (2002). Combining ability studies through diallel in pea (*Pisum sativum* L.). *Legume Res.* 25(2):105-108.
- Singh H, Singh M, Brar PS (2007). Assessment of combining ability for some quantitative characters in edible podded pea (*Pisum sativum* var. *macrocarpum*). *Crop Improvement*. 34(1):106-109.
- Singh HN, Srivastava JP, Singh SP (1972). Genetic variability and heritability in table pea (*Pisum sativum* L.). *Prog. Hort.* 4(3-4): 79-86.
- Singh JD, Singh IP (2003). Combining ability analysis in field pea. *Indian J. Pulses Res.* 16(2):98-100.
- Singh KP, Singh HC, Verma MC (2010). Genetic analysis for yield and yield traits in pea. *J. Food Legumes* 23(2):113-116.
- Singh KN, Santoshi US, Singh HG (1986). Genetics analysis of yield components and protein content in pea. *Indian J. Agric. Sci.* 56:757-764.
- Singh MN, Singh RB (1989). Genetics of earliness in pea. *Crop Improv.* 16:43-48.
- Singh NK, Kumar D, Kumar N, Singh DN (2001). Combining ability for yield and its components in pea. *Ann. Agric. Res.* 22(4):570-575.
- Singh RN, Mishra GM (1996). Heterosis and combining ability in pea (*Pisum sativum* L.). *Hort. J.* 9(2):129-133.
- Singh SP, Singh RP (1987). Diallel analysis for combining ability in pea. *Acta Agron. Hungarica* 36(1-2):89-95.
- Singh TH, Sharma RR (2001). Gene action for yield and its components in three crosses of pea (*Pisum sativum* L.). *Indian J. Genet. Plant Breed.* 61:174-175.
- Singh UP, Ganesh M, Srivastava CP (1997). Detection of epistasis and estimation of components of genetic variation applying modified triple test cross analysis using two testers in pea (*Pisum sativum* L.). *Indian J. Genet. Plant Breed.* 57:138-142.

- Singh YV, Ram HH (1988). F₂ diallel analysis of some quantitative traits in garden pea. Narenda Deva J. Agric. Res. 3:83-89.
- Sirohi A, Gupta VP, Sirohi A (1995). Inheritance of phonological and morphological traits in pea. Ann. Biol. Ludhiana 11:192-196.
- Sirohi A, Singh SK (2013). Studies on combining ability for leaf area, specific leaf weight and chlorophyll content in field pea. Adv. Plant Sci. 26(1):85-87.
- Sood M, Kalia P (2006). Gene action of yield related traits in garden pea (*Pisum sativum* L.). SABRAO J. Breed. Genet. 38(1):1-17.
- Sood M, Kalia P, Gautam G (2006). Heterosis, inbreeding depression and residual heterosis for pod yield, components traits and protein content in garden pea. Indian J. Hort. 63(4):460-463.
- Sprague GF, Tatum LA (1942). General vs specific combining ability in single crosses of corn. J. Am. Soc. Agron. 34:923-932.
- Srivastava CP, Singh RB (1988). Genetic analysis of seeds per pod in peas (*Pisum sativum* L.). Veg. Sci. 15:38-48.
- Srivastava PL, Joshi US, Singh HG (1986). Combining ability and heterosis in pea. Crop Improv. 13:20-23.
- Tysdal HM, Kiesselbech TA, Westover HL (1942). Alfalfa breeding. Nebr. Agric. Exp. Sta. Res. Bull. P. 124.
- Venkateswarlu S, Singh RB (1981). Heterosis and combining ability in peas. Indian J. Genet. 41:255-258.
- Zaman S, Hazarkia GN (2005). Combining ability in pea (*Pisum sativum* L.). Legume Res. 4:300-302.