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Study on gene effects for pod yield and horticultural traits of garden pea (*Pisum sativum* var. *hortense* L.) using trigenic model of generation mean analysis

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Abstract

The inheritance of pod yield and related horticultural traits of garden pea using 12 generations was followed in three inter-varietal crosses. The non-fixable gene effects are higher than the fixable as a consequence of higher magnitude of epistatic interactions. Duplicate type of epistasis for different traits in three crosses in one or the other environment suggested to proceed with mild selection intensity in the early generations followed by intense in the later. The failure of the trigenic model for shelling (%), pods/ plant, pod yield/ plant, pod length and seeds/ pod in all or in one of the crosses and environments revealed the complexity in the inheritance of these characters suggesting either presence of minor or modifier genes, and linkage rather than higher order interactions is responsible. The non-additive gene effects along with presence of non-allelic interactions for majority of the traits in respective crosses directed to adopt population improvement methods to break undesirable linkages through recombination or to defer selection in later generations following bulk pedigree or SSD methods with one or two inter-matings like recurrent selection.

Keywords: Garden pea, epistasis, trigenic interactions, duplicate epistasis, linkage.

Introduction

Garden pea (*Pisum sativum* var. *hortense* L., 2n=2x=14), a member of Fabaceae family, is one of the principal legume vegetable crops grown throughout the world. It is native of Mediterranean region with Near East and Ethiopia as secondary centres. It is a rich source of protein ranging from 23-33% (Sharma et al. 2019), slowly digestive starch, sugars and amino acids. Besides, it supplies an extraordinarily diverse health building nutrients such as vitamins, minerals and also lysine, a limiting essential amino acid in cereals (Sharma et al. 2019). The garden pea is used as fresh vegetable, pulse and processed as pickle, canned, frozen or dehydrated to consume during lean period (Sharma et al. 2019), thus making it an important food material. It helps to reduce the cost of production by fixing atmospheric nitrogen (Anjum et al. 2015) and provide the advantage of low input and sustainable farming. It is cultivated all through India especially in north-western Himalayan region, encompassing Himachal Pradesh, Uttrakhand and, Jammu and Kashmir states (Sharma et al. 2013) as off-season crop during the summer season and hence its cultivation is remunerative and provide rewarding economic profits to the farmers. The garden pea encounters many diseases during the crop season, particularly powdery mildew greatly affecting pod yield and, therefore, high yield of well filled-long-dark green-sweet pods and resistance to pests and diseases are the priority attributes for its genetic improvement.

Garden pea is an autogamous crop and recombinant breeding is the most appropriate approach to combine various desirable traits like long and lush green pods with high yield potential. The choice of appropriate plant breeding methodology for upgrading the yield potential largely depends upon the availability of reliable information on the nature and magnitude of gene effects present in the population (Shekhawat et al. 2006). Hence, an understanding of the inheritance of quantitative traits is essential to develop an efficient

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breeding strategy. Yield or any other related attributes are often controlled by number of genes with individually small but cumulative effects, averaged over the whole genome. The biometrical approaches should, therefore, suffice the genetic variance into additive, dominance and epistasis components. Generation mean analysis is a useful technique for the estimation of main gene effects (additive and dominance) and their digenic trigenic and other higher order interactions responsible for inheritance of quantitative traits. Its popularity in plant breeding and genetics continues unabated and helps to understand the performance of the parents used in crosses and potential of crosses to be used either for heterosis exploitation or pedigree selection (Dvojkovic et al. 2010). Although some studies have been conducted in garden pea in the past by using generation means to estimate the variance components, but these were based on only five or six generations and limited to the perfect fit model (Sharma and Sain 2004). Cavalli (1952) reported that accuracy of gene effects increase with increasing number of segregating generations and number of plants on which observations are to be taken. Therefore, present investigation was carried out by employing additive-dominance, digenic and trigenic models comprising of twelve generations to estimate the genetic effects for pod yield and horticultural traits in garden pea.

Materials and methods

Experimental materials and experimental sites

Twelve generations viz., P_1, P_2, F_1, F_2, B_1, B_2, B_{1S}, B_{2S}, B_{11}, B_{12}, B_{21} and B_{22} of three intervarietal crosses were developed by utilizing the four diverse parents namely, Palam Sumool, Punjab-89, Azad P-1 and Palam Priya. The F_1's and first backcross generations (B_1 and B_2) developed in winter 2011-12 and 2012-13, respectively and were raised during summer 2013 at Kukumseri (E_2) to develop second backcross generations (B_{11}, B_{12}, B_{21} and B_{22}) and their selfed progenies (B_{1S} and B_{2S}) under open field conditions. The seeds of these generations were multiplied by raising the respective populations at, Palampur (E_1) during winter 2013-14 under polyhouse conditions. Simultaneously, F_1's were backcrossed with their respective parents to increase the seeds of B_1 and B_2 generations. Seeds of second backcross generations were also multiplied in each cross combination.

Environment-1 (E_1) The Experimental Farm of CSKHPKV, Palampur, Himachal Pradesh, India is situated at an elevation of 1290.8 meters above mean sea level with 32°6´ N latitude and 76°3´ E longitude. The area is characterized by humid and sub-temperate climate (Zone-I), having severe winters and mild summers with high annual rainfall of 2500 mm of which 80 per cent is received during June-September. The soil is Alfisols typic-Hapludalf clay and is acidic in reaction (pH 5-5.6).

Environment-2 (E_2) The Experimental Farm of Highland Agricultural Research and Extension Centre, Kukumseri is situated at an elevation of 2672 meters above mean sea level with 31º44´15´´N latitude and 76º41´23´´E longitude. The area is characterized by dry temperate climate (Zone IV) with an annual rainfall of about 125 mm, gentle sloping mountains and a growing season from April to October. The soil is loamy sand with a pH of 6.7 and is skeletal mesic udic typic ustrothents.

Experimental layout

During *rabi*, 2014-15, the twelve generations viz., P_1, P_2, F_1, F_2, B_1, B_2, B_{1S}, B_{2S}, B_{11}, B_{12}, B_{21} and B_{22} was evaluated in Randomized Complete Block Design in three replications at Palampur (E_1). The sowing was undertaken by assigning single row to parents and F_1's, four rows to each backcross generations and six rows to F_2's and second cycle of backcross generations. The seeds were sown keeping inter and intra-row spacing of 45 cm and 10 cm, respectively in a row length of 2.5 m. All the intercultural operations were carried out in accordance with the recommended schedule (Anonymous 2009).

Data collection and statistical analysis

The data were recorded on 10 randomly selected competitive plants of each parents and F_1's, 20 plants in each backcross generations (B_1 and B_2) and second cycle of backcross generations (B_{11}, B_{12}, B_{21} and B_{22}), and 30 plants in each F_2's, B_{1S} and B_{2S}. The parameters recorded were days to flowering, days to first picking, pod length (cm), seeds/pod, shelling percentage, plant height (cm), pods/plant and pod yield/plant (g). Standard statistical procedures were used to obtain mean and variance for each generation separately. While calculating variances, the replicate effect was eliminated from total variances to obtain within replication variance were used to compute the standard error for each generation mean. The simple scaling tests (A, B, C and D) given by Mather (1949) and Hayman and Mather (1955) were followed for the detection of digenic interactions. The A, B, C and D values were calculated by the following formulae:

$$A = 2\overline{B}_1 - \overline{P}_1 - \overline{F}_1$$

$$B = 2\overline{B}_2 - \overline{P}_2 - \overline{F}_1$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$$

$$D = 2\overline{F}_2 - \overline{B}_1 - \overline{B}_2$$

The significant deviation of any of the scaling tests A, B, C and D from zero, indicates the presence of digenic interactions, otherwise adequacy of additive-dominance model was assumed.

Scaling tests for detecting of trigenic and higher order interactions were carried out as per Vander Veen (1959), by using formulae:

$$X = \tfrac{1}{2}\,(\overline{P}1 - \overline{P}2) - (\overline{B}11 + \overline{B}12) + (\overline{B}21 + \overline{B}22)$$

$$Y = F1 - \tfrac{1}{2}\,(\overline{P}1 + \overline{P}2) + (\overline{B}11 - \overline{B}12) - (\overline{B}21 - \overline{B}22)$$

The significant deviation of any of the scaling tests X and Y from zero, revealed the presence of trigenic or higher order interactions.

Estimation of various genic effects and test of fitness of appropriate genetic model was done according to Joint Scaling Test of Cavalli (1952), as described in detail by Mather and Jinks (1982). The estimation of genic effects and chi-square test of goodness of fit were carried out, using three-, six- and 10-parameter model. First, simple additive-dominance model consisting of (m), (d) and (h) gene effects was tried and the adequacy of this model was tested by the chi-square test. When this model failed to explain variation among generation means, successively non-allelic digenic interaction parameters i.e. (i), (j) and (l) were included in this model. Inadequacy of digenic interaction model led to the successive use of trigenic interaction model consisting of parameters namely, (w), (x), (y) and (z). Thus, all possible models with different combinations of epistatic parameters were tried to identify the best fit model with minimum or non-significant value of chi-square with maximum number of significant parameters as suggested by Mather and Jinks (1982).

Results and discussion

The analysis for variance of the 12 generations with three crosses namely, 'Palam Sumool × Punjab-89' (C_1), 'Palam Sumool × Azad P-1' (C_2) and 'Palam Sumool × Palam Priya' (C_3) revealed significant mean squares due to genotypes for days to first picking, pod length, shelling percentage, plant height, pods per plant and pod yield per plant in E_1 and for all the eight characters in E_2 . Thus, sufficient genetic variability existed in the genetic material involving different generations of three inter-varietal crosses under both the environments.

The F_1 hybrids showed better performance than their

Table 1. Analysis of variance with respect to three intervarietal crosses of garden pea for pod yield and various horticultural traits under two different environments

Cross	MSS	d.f		Days to flowering		Days to first picking		Pod length (cm)		Seeds/ pod		Shelling percentage		Plant height (cm)		Pods/ plant		Pod yield/ plant (g)	
		E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
C_1	Genotype	11	11	9.020	1.704*	122.181*	3.989*	1.714*	1.438*	1.350*	0.597*	47.182*	68.997*	187.271*	19.842*	6.663*	4.329*	283.967*	217.380*
	Error	22	22	9.194	0.818	8.719	0.482	0.121	0.254	0.248	0.136	10.544	4.117	10.481	4.279	0.388	0.229	22.039	8.702
C_2	Genotype	11	11	0.977	1.300*	24.694*	4.431*	2.850*	2.621*	0.379	1.486*	60.600*	55.492*	249.061*	13.600*	12.456*	2.047*	1056.153*	81.835*
	Error	22	22	2.727	0.712	4.626	1.356	0.435	0.159	0.278	0.168	7.926	2.984	7.629	2.086	0.926	0.176	18.736	9.111
C_1	Genotype	11	11	3.422*	2.545*	19.868*	2.656*	2.654*	3.029*	0.291	0.468*	66.720*	40.226*	105.538*	45.480*	21.719*	8.040*	126.031*	115.517*
	Error	22	22	1.073	0.856	4.694	0.224	0.491	0.061	0.291	0.094	12.551	3.007	20.905	4.246	0.501	0.216	10.597	2.869

MSS = Mean Sum Square, df = Degree of Freedom, *Significant at 5% level, C_1 = Palam Sumool × Punjab-89, C_2 = Palam Sumool × Azad P-1, C_3 = Palam Sumool × Palam Priya, E_1 = Environment 1 and E_2 = Environment 2 respective parents in desirable direction in all the crosses for most of the traits except for shelling percentage for C_2 under both the environments and plant height under E_1 (all three crosses) and E_2 (C_1 and C_2) for which the respective crosses showed inferior performance compared to either P_1 or P_2 or both the parents. In all the three crosses across all the generations days to flowering ranged from 47 to 51 days in Kukumseri (E_2) to 83 to 94 days at Palampur (E_1); days to first picking from 64 to 69 days in E_2 to 123 to 148 in E_1; pod length from 8 to 12 cm in E_2 to 9,6 to 12 .7 cm in E_1; plant height from 27 to 41 cm in E_2 to 76 to 110 cm in E_1; pods per plant from 4-9 in E_2 to 6 to 16 in E_1; and pod yield/plant from 25 to 56 g in E_2 to 42 to 106 g in E_1. There was not much in shelling per cent which ranged from 38 to 57 per cent in E_2 to 37 to 52 per cent in E_1. The two environments were thus drastically diverse.

The results obtained on estimates of scaling tests for detection of digenic and trigenic interactions and various genic effects of two environments (E_1 and E_2) are presented in Table 1 and 2. Genetic inheritance of various horticultural traits varied trait-wise as well as cross-wise. Earliness in flowering and days to first picking is highly desirable attribute in vegetables as the prices are perpetually high in early season in the market. For days to flowering, non-significance of 'A', 'B', 'C' and 'D' scaling tests and chi-square values for all the three crosses (C_1, C_2 and C_3) in E_1 indicated adequacy of simple additive-dominance model and absence of non-allelic interactions whereas, significance of X in cross (C_1), C in (C_2) and B, C an D in (C_3) indicating the role of non-allelic interactions in inheritance of this trait under environment 2. Further, significance of chi-square in cross (C_3) in environment 2 showed the inadequacy of additive-dominance and digenic model, respectively which might be due to the presence of linkage among interacting genes or trigenic or higher interactions in the respective crosses. The estimates of genic effects showed negative and significant additive (d) gene effect in the crosses (C_2) and (C_3) in E_1, whereas, the genic effects revealed the significance of 'j' and 'y' components in (C_3) and (C_1), respectively under E_2 indicating greater role of these non-allelic interactions in the inheritance of days to flowering.

On the other hand, non-allelic interactions were observed for the inheritance of days to first picking in all the three crosses under both environments. The scaling tests for digenic interactions revealed the significance of 'A' and 'B' scales in (C_2) under (E_1) and 'B', 'C' and 'D' scales in cross (C_3) under (E_2) indicating the presence of all the three types of non-allelic interactions viz., (i), (j) and (l) while, only 'A' scale was significant in cross (C_1) and (C_3) under environment 2 and environment 1, respectively indicating the presence of 'i' type interaction. Further, the scaling tests for trigenic interaction indicating the significance of 'X' in cross (C_2) and (C_3), 'Y' in (C_1) under (E_1) and that of 'X' and 'Y' both in cross (C_2) under (E_2), revealed the presence of trigenic or higher order interactions. The estimates of genic effects including interactions revealed that additive (d) gene effect was positive and significant in (C_2) which was further corroborated by negative and significant additive × dominance (j) and significant and positive additive × dominance × dominance (y) genic interactions. Similarly, the significance of additive × dominance × dominance (y) with positive sign and that of dominance × dominance × dominance (z) with negative sign in cross (C_2) and (C_3) under (E_2) and (E_1), respectively. In addition, the non-significance of chi-square showed the adequacy of trigenic interaction model in all the cross combinations in (E_1) whereas, the inadequacy of digenic interaction model was observed as revealed from the significant values of chi-square under (E_2) for (C_3) cross.

Non-significance of all 'A', 'B', 'C', 'D', 'X' and 'Y' scales in all the three crosses for pod length under (E_1); for seeds per pod under (E_2) in all the three crosses and for two crosses i.e. (C_2) and (C_3) in (E_1) indicated the adequacy of additive-dominance model and absence of digenic or higher order non-allelic interactions. However, significance of 'C' scale in cross (C_1) for pod length and seeds per pod under (E_2) and (E_1), respectively indicated the importance of 'l' type non-allelic interaction. Further, significance of chi-square in cross (C_3) for pod length and cross (C_1) for seeds per pod in both the environments showed the inadequacy of additive-dominance and digenic model, respectively and presence of linkage among interacting genes or trigenic or higher interactionsn the respective crosses. Genic interactions for pod length in crosses (C_1) and (C_2) in both the environments showed significant and positive additive (d) effect. However, significance of both additive (d) and dominance (h) gene effects was noticed in crosses (C_1) and (C_2) under (E_2) and (C_2) in (E_1). For seeds per pod, additive (d) genic effects were found to be negative and significant in (C_1) in both the environments. However, opposite sign of 'h' and 'l' components in cross (C_1) under (E_1) indicated duplicate epistasis. The genic effects

Table 2. Estimates of various genic effects and non-allelic interactions effects with respect to three intervarietal crosses of garden pea for pod yield and various horticultural traits under two different environments

Genic effects	Cross(s)/ Trait(s)/ Environment(s)											
	C_1		C_2		C_3		C_1		C_2		C_3	
	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
	Days to flowering						Days to first picking					
A	1.33±2.85	-0.33±1.05	3.00±4.24	1.33±0.94	-0.33±3.07	-2.00±1.41	-12.67±7.28	-4.33*±2.05	-6.67*± 3.02	3.33±2.79	-8.67*±3.64	-2.00±1.41
B	3.33±3.62	1.67±1.94	1.00±3.65	0.33±0.94	-1.67±2.36	-2.67*±0.94	0.67±7.27	0.67±1.70	10.33*±3.40	-1.67±1.56	3.33±2.00	-2.67*±0.94
C	-13.33±12.12	0.00±2.71	3.33±4.22	3.67*±1.70	-6.67±4.82	-4.00*±1.89	-9.33±16.26	1.00±4.29	1.00±5.12	3.67±3.09	-16.67±8.81	-4.00*±1.89
D	-9.00±5.35	-0.67±1.49	-0.33±3.18	1.00±0.82	-2.33±2.31	0.33*±0.94	1.33± 8.94	2.33±1.94	-1.33±2.45	1.00±1.73	-5.67±4.25	0.33*±0.94
X	1.00±5.20	4.33*±0.73	-0.33±2.94	-0.17±1.40	0.67±2.58	0.34±1.46	6.01±6.75	4.00±2.20	14.18*±3.96	4.67*±1.78	7.66*±2.77	0.34±1.46
Y	-1.68±5.78	0.67±0.93	-0.67±3.10	-0.84±1.44	-0.34±3.00	-1.67±1.57	-14.68*±6.95	-0.67±2.41	0.84±4.24	-4.34*±1.91	-5.66±3.28	-1.67±1.57
m	88.36*±0.78	50.11*±3.89	89.01*±0.35	49.79*±0.88	92.69*±0.46	48.59*±1.25	136.64*±23.32	66.75*±1.87	143.05*±9.17	76.86*±6.09	156.36*±12.63	48.59*±1.25
(d)	1.06*± 0.43	0.62±3.00	-6.24*±0.36	0.35±0.36	-1.56*±0.46	-0.60±0.31	6.55±16.46	0.96± 0.70	15.67*±7.46	1.11±5.56	0.68±9.61	-0.60±0.31
(h)	-0.74± 1.63	-8.43±19.93	-0.62±0.93	-0.40±2.48	-1.39±1.01	0.38±3.43	-54.85±123.35	-5.27±4.85	-3.10±46.90	-50.92±28.02	-86.50±63.21	0.38±3.43
(i)	-	-2.07±3.90	-	-1.26±0.94	-	2.02±1.24	-0.20±23.35	-1.58±1.94	-0.90±9.18	-10.56±6.11	-8.37±12.63	2.02±1.24
(j)	-	-12.86±8.05	-	1.16±1.16	-	3.27*±1.21	-27.20±44.97	-2.70±2.16	-73.88*±22.53	-9.20±13.03	-27.95±21.53	3.27*±1.21
(l)	-	10.43±30.26	-	-0.94±1.80	-	1.33±2.53	105.90±188.15	4.00±3.55	4.81±75.76	78.58±40.65	157.38±91.71	1.33±2.53
(w)	-	0.41±2.99	-	-	-	-	4.67±16.39	-	-9.82±7.42	-0.82±5.47	-0.28±9.60	-
(x)	-	6.84±11.31	-	-	-	-	-13.21±71.82	-	6.04±22.88	19.60±15.06	46.04±37.59	-
(y)	-	23.86*±7.41	-	-	-	-	28.08±44.56	-	84.20*±24.89	22.27*±10.76	37.94*±15.94	-
(z)	-	-4.08±14.53	-	-	-	-	-63.97±89.06	-	-2.84±38.78	-40.8*±19.07	-82.55*±41.95	-
χ^2	8.15	0.50	2.04	6.50	4.36	13.08*	1.18	11.19	0.09	4.56	2.37	13.08*
A	1.55±0.86	-1.73±1.43	-1.00±0.83	0.70±0.51	2.59±1.43	-1.35*±0.25	0.93±1.46	0.35±0.41	-0.05±0.55	-0.25±0.32	1.17±0.85	0.45±0.76
B	1.38±0.98	1.20±0.99	-1.86±1.04	1.40*±0.27	1.28±1.27	0.55*±0.27	0.29±0.40	0.15±0.75	0.93±0.86	-0.60±0.79	-0.66±0.61	0.15±0.25
C	1.04±2.89	-2.10*±1.06	0.47±2.05	0.90±0.79	3.06±2.82	-1.00±0.95	4.09*±0.80	1.10±1.40	1.02±1.34	-0.15±1.23	-0.22±2.53	-0.20±0.84
D	-0.95±1.42	-0.78±0.85	1.67±0.93	-0.60±0.34	-0.41±1.58	-0.10±0.49	1.44±0.77	0.65±0.74	0.07±0.74	0.35±0.69	-0.37±1.31	-0.40±0.56
X	0.16±0.78	0.51±0.58	-0.52±1.54	-0.22±0.64	0.34±0.76	-0.20±0.43	0.55±0.49	0.79±0.43	-0.70±0.70	-1.30*±0.45	0.27±0.52	0.41±0.25
Y	-0.91±0.90	-0.46±0.72	0.76±1.64	-0.68±0.68	0.46±0.83	1.21*±0.44	0.79±0.52	-0.85±0.55	0.44±0.75	-1.99*±0.46	-0.24±0.55	0.63*±0.25
m	11.42*±0.20	9.52*±0.52	10.74*±0.16	9.56*±0.34	11.14*±0.16	8.78*±1.13	9.51*±0.38	7.05*±0.02	6.89*±0.11	6.44*±1.70	6.19*±0.11	10.16*±1.30

(d)	0.95* ±0.19	1.27*±0.19	1.33*±0.15	1.44*±0.15	1.36*±0.15	-0.28±0.53	-0.47* ±0.18	-0.50*±0.02	-0.23*±0.11	-2.00±1.22	-0.34*±0.10	3.49*±1.01
(h)	0.54± 0.37	0.89*±1.62	1.11*±0.44	3.71*±0.98	-0.20±0.35	5.63±6.47	-5.19*±1.11	-0.65*±0.13	-0.24±0.23	2.04±8.79	-0.04±0.22	-12.49±6.44
(i)	-	0.69±0.48	-	0.67±0.38	-	1.28±1.13	-2.81*±0.41	-	-	1.26±1.70	-	-3.48*±1.30
(j)	-	-2.27*±0.77	-	-0.98*±0.44	-	-0.01±1.69	-0.94±0.54	-	-	6.67*±3.08	-	-7.97*±2.28
(l)	-	0.48±1.31	-	-2.58*±0.79	-	-10.61±10.09	2.51*±0.87	-	-	5.06±12.96	-	14.06±9.27
(w)	-	-	-	-	-	2.31*±0.53	-	-	-	1.12±1.21	-	-3.76*±1.00
(x)	-	-	-	-	-	-2.25±3.98	-	-	-	-4.81±5.27	-	8.06*±3.83
(y)	-	-	-	-	-	1.68±2.05	-	-	-	-7.18*±2.63	-	6.33*±1.68
(z)	-	-	-	-	-	6.04±4.79	-	-	-	-4.99±5.89	-	-4.72±4.12
χ^2	14.67	2.25	15.32	11.13	18.30*	19.22*	25.84*	26.91*	13.37	5.83	12.63	23.88*
A	1.53±4.23	-7.30*±0.93	-1.73±3.46	-10.05*±2.56	-0.18±5.49	-14.6*±2.19	6.30±6.91	5.00±2.57	-29.83*±7.10	3.40±2.32	-21.21*±5.46	7.90±6.80
B	5.63±4.45	3.90±4.25	-0.62±4.21	5.75±4.08	0.45±5.35	5.75±3.19	-19.43*±6.09	9.53*±4.44	-17.19*±5.68	4.60±2.67	-19.52*±6.52	4.60±3.21
C	-24.98*±7.04	-14.50±8.74	15.01±11.11	-2.50±4.91	13.53*±5.90	-13.0*±4.50	-8.93±13.85	4.60±3.89	-3.57±8.00	-8.40±4.55	-35.87*±11.39	-9.00*±1.52
D	-16.07*±3.90	-5.55±4.83	8.68±5.56	0.90±1.87	6.63±3.47	-2.10±2.77	2.10±7.83	-4.97*±2.46	21.72*±4.60	-8.20*±1.35	2.43±5.87	-10.75*±3.70
X	-0.42±4.74	11.10*±2.44	-3.85±5.35	-3.71*±0.99	-6.94±4.93	1.01±2.74	-2.82±5.37	3.24±2.54	-36.87*±5.05	-0.55±3.44	13.73*±4.86	-7.60*±2.47
Y	-3.48±5.01	2.60±2.53	-1.57±5.57	-9.25*±2.81	-8.31±5.42	1.62±2.91	-2.73±5.73	-3.90±3.07	21.56*±5.74	4.34±4.05	10.67*±5.37	-4.40±2.49
m	30.83*±4.72	33.88*±9.78	41.47*±0.94	36.23*±4.34	39.41*±3.84	57.00*±1.77	57.60*±5.79	27.28*±2.15	54.34*±15.10	27.02*±1.93	56.72*±20.18	69.77*±5.67
(d)	-4.58*±1.13	-13.30*±4.30	-4.69*±0.93	-8.85*±3.88	-4.77*±1.18	-2.42*±0.18	2.37*±0.90	2.70*±0.61	-30.35*±13.57	1.39*±0.73	33.46±17.26	20.85*±5.62
(h)	28.14*±12.7	45.37±56.32	7.65*±1.74	35.63±20.49	17.06±12.38	-32.19*±4.61	94.92*±14.6	18.97*±6.29	283.97*±71.61	27.38*±5.59	168.95±96.16	-181.25*±25.80
(i)	11.49*±4.74	16.89±9.78	-	12.27*±4.35	0.91±3.80	-10.02*±1.79	27.31*±5.85	2.63±2.00	42.71*±15.12	10.04*±1.92	39.34±20.22	-35.65*±5.69
(j)	0.41±4.60	-16.59±13.24	-	12.94±8.41	-3.94±5.00	-4.22*±1.44	13.29*±4.41	-3.86±2.67	166.45*±35.25	1.40±2.16	-90.06*±40.75	-10.94±16.12
(l)	-12.18±9.00	-52.14±85.24	-	-33.36±32.48	-6.33±9.81	22.97*±3.38	-61.61*±10.2	-12.8*±4.94	-515.64*±109.49	-18.41*±4.93	-278.2*±140.63	265.16*±38.94
(w)	-	9.61*±4.30	-	4.97±3.85	-	-	-	-	27.15*±13.52	-	-32.24±17.99	-19.31*±5.59
(x)	-	-15.23±35.73	-	-24.40*±11.11	-	-	-	-	-210.59*±36.25	-	-108.70*±53.24	96.64*±11.43
(y)	-	44.84*±13.22	-	-32.59*±5.95	-	-	-	-	-261.38*±32.63	-	98.80*±33.66	-27.77±14.66
(z)	-	21.94±38.88	-	13.23±18.30	-	-	-	-	285.66*±54.64	-	155.66*±65.78	-123.39*±19.10
χ^2	14.01*	4.41	22.98*	17.47*	63.84*	35.33*	63.41*	12.92*	22.57*	20.78*	5.55	21.92*
A	-2.45*±0.74	5.50*±0.57	-6.67*±0.98	1.80*±0.27	-1.16±1.20	5.00*±1.54	-8.23±6.08	35.50*±3.66	-78.45*±3.67	-2.00±3.79	3.69±7.24	14.50*±2.72
B	3.99*±0.67	3.10*±0.45	-3.50*±1.73	1.40*±0.52	-9.47*±1.98	4.90*±0.43	13.99*±4.84	17.00*±3.56	-38.21*±7.73	-11.50*±4.94	5.65±5.92	21.00*±3.70
C	10.47*±2.67	6.00*±0.86	-7.27*±2.62	1.80*±0.48	-6.13*±2.45	4.10*±1.56	66.33*±14.81	18.50*±6.06	-74.33*±12.22	-14.50±9.40	58.27*±11.68	11.50*±2.78

D	4.46*±1.29	-1.3*±0.45	1.45±1.15	-0.70*±0.26	2.25±1.16	-2.90*±1.03	30.28*±7.89	-17.00*±3.08	21.16*±6.09	-0.50±3.97	24.46*±7.05	-12.00*±2.16
X	-0.85±0.91	1.37*±0.63	0.29±1.02	-0.10±0.76	-3.41*±0.89	2.51*±0.91	-7.33±7.07	7.50±4.47	6.76±4.61	2.01±3.09	2.34±5.48	9.18±5.09
Y	-2.53*±0.99	0.05±0.66	4.15*±1.21	-0.84±0.78	-0.73±1.24	0.78±1.00	-22.23*±7.17	2.83±4.90	35.57*±5.31	4.34*±0.78	-10.67*±5.36	2.83±5.26
m	2.25±3.15	7.80*±2.21	7.12*±3.53	3.41*±0.44	11.37*±2.53	10.43*±2.51	-5.18±20.79	21.57*±3.60	31.08±19.15	45.20*±11.3	-14.90±21.07	24.17*±3.29
(d)	0.31±1.66	-6.89*±2.06	-6.03*±2.87	-0.52*±0.12	-4.01*±1.84	0.78±1.93	-24.31±13.64	0.83±0.85	-11.04±15.71	-30.25*±8.56	25.28±17.39	-1.92*±0.51
(h)	35.43*±17.8	-10.95±9.82	26.22±17.52	7.71*±1.28	-3.66±13.61	-15.35±12.89	286.33*±112.94	72.17*±9.61	286.24*±93.21	-17.03±57.62	245.77*±103.3	62.60*±9.76
(i)	5.74±3.16	-3.78±2.22	1.68±3.55	1.90*±0.43	4.79±2.54	-4.28±2.51	62.72*±20.81	6.47±3.51	36.93±19.18	-3.73±11.34	40.44±21.10	13.44*±3.25
(j)	-4.49±5.21	13.14*±4.79	7.77±7.38	-0.05±0.46	9.56±5.21	-13.40*±5.30	56.99±40.73	1.21±3.62	-16.07±37.39	57.23*±21.2	-61.65±43.45	-12.85*±3.36
(l)	-44.38±27.5	23.18±13.78	-63.44*±26.3	-5.29*±0.91	5.39±22.12	23.33±19.90	-287.72±175.30	-45.83*±6.99	-610.00*±136.50	30.74±87.28	-306.9*±153.1	-41.82*±6.89
(w)	-1.06±1.66	6.45*±2.06	4.54±2.84	-	-0.84±1.80	-2.72±1.93	28.94*±13.59	-	22.26±15.62	29.09*±8.54	-26.69±17.36	-
(x)	-27.0*±10.7	10.28*±5.03	-18.76±9.88	-	-7.01±7.80	17.91*±7.03	-196.39*±65.28	-	-285.86*±52.76	1.79±33.28	-171.86*±57.6	-
(y)	-4.03±5.86	-5.91±3.69	-1.63±6.51	-	-14.93*±5.45	16.90*±5.32	-32.15±43.96	-	110.17*±31.03	10.79±16.83	35.57±37.97	-
(z)	15.49±13.07	-14.57*±6.26	42.75*±12.66	-	-0.20±11.62	-12.69±9.69	65.70±83.90	-	390.68*±63.54	-3.18±42.87	112.14±71.56	-
χ^2	57.50*	25.69*	28.66*	50.70*	17.27*	2.42	40.93*	79.90*	214.58*	22.87*	0.52	70.53*

C_1 = Palam Sumool × Punjab-89, C_2 = Palam Sumool × Azad P-1, C_3 = Palam Sumool × Palam Priya, E_1 = Environment 1 and E_2 = Environment 2, m= mean, (d) = additive, (h) = dominance, (i) = additive × additive, (j) = additive × dominance, (l) = additive × dominance, (w) = additive × additive × additive, (x) = additive × additive × dominance, (y) = additive × dominance × dominance, (z) = dominance × dominance × dominance, $\div^2$= Chi square value, *Significant at 5% level of significance

revealed the significance of 'i', 'j', 'w', 'x' and 'y' components in cross (C_3) under (E_2) indicating greater role of these non-allelic interactions in the inheritance of seeds per pods.

With respect to shelling percentage, 'A' scale was significant in all the three cross under (E_2) whereas, 'C' scale was significant in crosses (C_1) under (E_1) and in cross (C_3) under both the environments indicated the presence of 'l' type epistatic interactions,. The presenceof trigenic and higher order interactions was revealed by the significant values of 'X' and 'Y' scaling tests in cross (C_2) in (E_2). The digenic model revealed the significance of dominance (h) gene effects in crosses (C_1) and (C_2) which was also corroborated by negative additive (d) gene effects in both the crosses and also in (C_3) under E_1. The genic effects revealed the significance of 'i', 'j', and 'l' in (C_3), 'x', 'y' in (C_2) and 'w' and 'y' components in (C_1) indicating greater role of these non-allelic interactions in the inheritance of shelling percentage under E_2. Further, the inadequacy of digenic and trigenic interaction model was observed as revealed from the significant values of chi-square in C_1 and C_3 (E_1) and C_2 (E_2), respectively.

For plant height, simple additive-dominance model was inadequate as revealed from the significance of either of 'A', 'B', 'C' and 'D' scaling tests in all the three crosses in both the environments, indicating the presence of 'i', 'j' and 'l' digenic epistatic interactions. The presence of trigenic or higher order interactions were observed for the crosses (C_2) and (C_3) as revealed from the significance of 'X' and 'Y' scales under E1 and only 'X' scale in cross C_3 under E_2. The opposite signs of 'h' and 'l' showed the presence of duplicate type of epistatic interactions in both E_1 (C_1 and C_2) and E_1 (C_2 and C_3) environments. Further, in cross (C_2), the direction of dominance × dominance (l) at digenic level changed to positive dominance × dominance × dominance (z) non-allelic interaction indicated a shift from duplicate to complementary type of epistasis at higher order interactions. The genic effects revealed the significance of 'l', 'x' and 'z' components in (C_3) under both the environments indicating greater role of these non-allelic interactions in the inheritance of plant height. Chi-square values were significant showing the inadequacy of digenic interaction model under both the environments for C_1 and under E_2 for C_2 and that of trigenic interaction model in crosses C_2 (E_1) and C_3 (E_2).

With respect to number of pods per plant and pods yield per plant, significance of either of ‘A’, ‘B’, ‘C’ and ‘D’ parameters for all the three crosses under both the environments indicated the inadequacy of additive-dominance model and showed the presence of ‘i’, ‘j’ and ‘l’ type of non-allelic interactions. Further, the significance of ‘Y’ in majority of three crosses for pod yield per plant and pods per plant except significance of ‘X’ in (C_3) for pods per plant implies the presence of trigenic and higher order interactions under environment 1. Significance of ‘X’ was observed under E_2 for crosses C_1 and C_3. Genic interactions for pods per plant showed the significance of dominance (h) gene effect along with negative higher order additive gene interaction (w) in cross (C_1) while, the other two crosses revealed negative and significant additive (d) genic effects. Further, it was observed that negative and significant ‘l’ type of interaction converted to positive and significant dominance × dominance × dominance (z) type interaction at trigenic level in (C_2) suggesting that both parents possessed heterozygous loci with dominant alleles. Genic interactions under environment 2 possessed the significant and negative additive (d) effect in crosses C_1 and C_2 The genic effects revealed the significance of ‘j’, ‘w’, ‘x’ and ‘z’ components in cross C_1 and ‘j’, ‘x’ and ‘y’ in cross C_3 indicating greater role of these non-allelic interactions in the inheritance of pods per plant. In addition, the inadequacy of trigenic interaction model was observed as revealed from the significant values of chi-square under both the environments for C_1 cross.

The genic effects for pod yield per plant revealed that the trigenic interactions contributed more than the digenic interactions in controlling the inheritance of this trait. The significant and positive ‘i’ and ‘w’ type non-allelic interactions in cross (C_1) indicated the presence of increaser alleles along with associated pair of genes. Dominance (h) interaction was found to be positive and significant in crosses C_1 and C_3 under both the environments. On the other hand, duplicate epistasis based on digenic interactions was observed in crosses (C_2) and (C_3) under E_1 and in C_3 under E_2. However, the direction of magnitude of ‘l’ type digenic interaction has improved to positive and significant ‘z’ type trigenic epistasis in cross (C_2) under environment E_1. Significance of chi-square values revealed the non-fitness of trigenic interaction model in crosses C_1 and C_2 under E_1 and digenic model in crosses C_1 and C_3 under E_2.

Results of absolute totals of fixable [(d), (i) and (w)] and non-fixable [(h), (j), (l), (x), (y), and (z)], gene effects revealed that non-fixable gene effects were many times higher than the fixable gene effects in all the three crosses (C_1, C_2 and C_3) in both the environments (E_1 and E_2) confirming that non-additive gene effects had a very important role in the inheritance of characters namely, days to first picking, shelling percentage , plant height, pods per plant and pod yield per plant (Table 3). Seeds per pod had also showed high value for non-fixable gene effect in crosses C_1 and C_2 in E_1 and E_2.

The results obtained in the present set of materials in general showed the presence of non-additive gene action for the inheritance of different traits under both the environments. Conflicting reports on the inheritance of yield and its component traits in pea are available in the literature using different biometrical approaches other than generation mean analysis (Sharma and Kalia 2002; Sharma et al. 2004; Thakur and Khosla 2008; Punia et al. 2013, Thiyam et al. 2013). In contrary, the importance of both additive and non-additive gene actions were reported by Sharma et al. (2004), Sharma et al. (2007), Sharma and Sharma (2012), Nassef and El-Rawy (2013) and Sharma et al. (2015) using different biometrical approaches and different genetic materials to study the inheritance of different characters. Raikwar (2019) also reported the importance of both additive and non-additive gene actions for most of the characters studied in wheat.

In this selection intensity should be mild in the earlier and intense in the later generations because it marks progress through selection (Sharma and Sain 2002). It is also suggested that an appropriate choice of environment should be made so that the characters will show relative inheritance for further increase of pod yield in garden pea.

In garden pea, the improvement of different quantitative traits warrants for a breeding methodology which can capitalize fixable (d + i + w) and non-fixable (h + j + l + x + y + z) gene effects. Therefore, normal breeding methods would not be fruitful rather than the methods which will exploit non-additive gene effects and take care of non-allelic interactions such as restricted recurrent selection by way of inter-mating the most desirable segregates followed by selection (Joshi 1979) or some forms of recurrent selections like diallel selective mating (Jensen 1970) or biparental mating in early segregating generations (Singh et al. 2008) could be promising for the genetic improvement

Table 3. Absolute totals of epistatic effects, fixable and non-fixable gene effects with respect to three intervarietal crosses of garden pea for pod yield and various horticultural traits under two different environments

Cross	Env.	Main effects (d)	Epistatic effects (h)	Total gene effects I order	II order	Fixable	Non-fixable
Days to flowering							
C_1	E_1	1.06	-0.74	-	-	1.06	0.74
	E_2	0.62	-8.43	25.35	31.11	-	-
C_2	E_1	-6.24	-0.62	-	-	6.24	0.62
	E_2	0.35	-0.40	3.36	-	1.61	2.5
C_3	E_1	-1.56	-0.60	-	-	1.56	1.39
	E_2	-1.39	0.38	6.80	-	2.80	4.98
Days to first picking							
C_1	E_1	6.55	-54.85	133.30	109.93	11.42	293.21
	E_2	0.96	-5.27	8.28	-	2.54	11.97
C_2	E_1	15.67	-3.10	79.59	102.90	26.39	174.87
	E_2	1.11	-50.92	89.34	171.80	12.49	210.95
C_3	E_1	0.68	-86.50	193.70	166.81	9.33	438.36
	E_2	-0.60	0.38	6.80	-	2.62	4.98
Pod length (cm)							
C_1	E_1	0.95	0.54	-	-	0.95	0.54
	E_2	1.27	0.89	3.44	-	1.96	3.64
C_2	E_1	1.33	1.11	-	-	1.33	1.11
	E_2	1.44	3.71	4.23	-	2.11	7.27
C_3	E_1	1.36	-0.20	-	-	1.36	0.20
	E_2	-0.28	5.63	11.90	12.28	130.59	26.22
Seeds/ pod							
C_1	E_1	-0.47	-5.19	6.26	-	3.28	8.64
	E_2	-0.50	-0.65	-	-	0.50	0.65
C_2	E_1	-0.23	-0.24	-	-	0.23	0.24
	E_2	-2.00	2.04	12.99	18.10	4.38	30.75
C_3	E_1	-0.34	-0.04	-	-	0.34	0.04
	E_2	3.49	-12.49	25.51	22.87	10.73	53.63
Shelling percentage							
C_1	E_1	-4.58	28.14	24.71	-	16.07	40.77
	E_2	-13.30	45.37	85.62	91.17	39.80	196.11
C_2	E_1	-4.69	7.65	-	-	4.69	7.65
	E_2	-8.85	35.63	58.57	75.19	26.09	152.18
C_3	E_1	-4.77	17.06	11.18	-	5.68	27.33
	E_2	-2.42	32.19	37.21	-	12.44	65.18
Plant height (cm)							
C_1	E_1	2.37	94.92	102.21	-	29.68	169.82
	E_2	2.70	18.97	19.37	-	5.33	35.71
C_2	E_1	-30.35	283.97	724.80	784.75	100.21	1722.69
	E_2	1.39	27.38	29.85	-	11.43	47.19
C_2	E_1	33.46	168.95	461.63	395.4	105.04	900.400
	E_2	20.85	-181.25	311.75	267.11	75.81	705.15
Pods/ plant							
C_1	E_1	0.31	35.43	54.61	47.60	7.11	130.84
	E_2	-6.89	-10.95	40.10	37.21	17.12	78.03
C_2	E_1	-6.03	26.22	72.89	67.68	12.25	160.57
	E_2	-0.52	7.71	7.24	-	2.42	13.05
C_2	E_1	-4.01	-3.66	19.74	22.98	9.64	40.75
	E_2	0.78	-15.35	41.01	50.22	7.78	99.58
Pod yield/ plant (g)							
C_1	E_1	-24.31	286.33	407.43	323.18	115.97	925.28
	E_2	0.83	72.17	53.51	-	7.30	119.21
C_2	E_1	-11.04	286.24	663.00	808.97	70.23	1699.02
	E_2	-30.25	-17.03	91.70	44.85	63.07	120.76
C_2	E_1	25.28	245.77	409.03	346.26	92.41	933.93
	E_2	-1.92	62.60	68.11	-	15.36	117.27

C_1 = Palam Sumool × Punjab-89, C_2 = Palam Sumool × Azad P-1, C_3 = Palam Sumool × Palam Priya, E_1 = Environment 1 and E_2 = Environment 2, First order interaction: [(i), (j), (l)], second order interactions: [(w), (x), (y), (z)], fixable components: [(d), (i), (w)], non-fixable components: [(h), (l), (x), (y), (z)]

of yield and associated traits. In addition, few cycles of recurrent selection followed by pedigree method may also be useful for the effective utilization of all three types of gene effects simultaneously. It will lead towards an increased variability in later generations for effective selection by maintaining considerable variability through mating of selected plants in early segregating generations.

However, silver lining in the present material was the adequacy of additive-dominance model for all the three crosses for pod length and for two crosses i.e. C_2 and C_3 in E_1. This provides for an opportunity to do extensive selection for these two yield contributing traits in early generations to exploit the fixable additive gene action and additive x additive gene interactions in E_1 location (Sareen et al. 2018). Similarly adequacy of additive-dominance model for seeds per pod in all the three crosses in E_2 can also be exploited by selection in early generations at E_2. Raikwar (2019) also reported the similar results in wheat. Based on this variation in gene action due to g×e interaction we suggest that the early generation materials be selected in the target environment. It was also observed that both additive-dominance and digenic interaction model appeared to be inadequate for days to first picking, plant height, pods per plant and pod yield per plant in one or the other or all three crosses under E_1 or E_2. Based on chi-square test for goodness of fit, it was evident that the decrease in chi-square values brought about by trigenic epistasis was manifold in comparison with others. Even in trigenic epistasis model was unable to account for all the variations among generation means for majority of the traits namely, pods per plant and pod yield per plant among different crosses. Mather and Jinks (1971) was of the view that if a model which allows for both digenic and trigenic interactions among unlinked genes is also inadequate, linkage rather than higher order interactions is responsible for the failure of digenic interaction model. This mean that digenic interactions between linked pair of genes give a satisfactory description of differences among the generation means.

Therefore, as suggested above, the use of population improvement method may be useful for generating additive variability by breaking undesirable linkages through greater recombination. In these approaches, a large number of crosses are required to be attempted, which is a difficult proposition in self pollinated crops. The other alternative can be to defer selection in the later generations by advancing segregating material through bulk pedigree or single seed descent method or single pod descent method with one or two inter-mating like recurrent selection (Sharma et al. 2012, Sharma et al. 2013 and Sareen et al. 2018). During the process, non-additive gene action may constantly be converted into additive gene action due to frequent opportunity for recombination. By deferring selection to the later generations (Fasoulas 1981) all the non-additive effects are constantly converted through recombination into additive and fixable effects and vice-versa.

Authors' contribution

Conceptualization of research (AS); Designing of the experiment (AS); Contribution of the experimental materials (AS); Execution of field/ lab experiments and data collection (KS, AS); analysis of data and interpretations (AS, KS); Preparation of manuscript (KS, AS).

Declaration

The authors declare no conflict of interest.

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