

RESEARCH ARTICLE

Gene interactions and genetics for yield and its attributes in grass pea (*Lathyrus sativus* L.)

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Abstract

Grain yield is a complex character representing a multiplicative end product of many yield attributes. However, understanding the genetics and inheritance that underlies yield and its component characters pose a prerequisite to attain the actual yield potential of any crop species. The knowledge pertaining to gene actions and interactions is likely to direct and strengthen the crop breeding programmes. With this objective, the present investigation was undertaken by using six generations derived from three different crosses in grass pea. The study underscores the significance of additive–dominance model, gene action involved in inheritance of quantitative characters and heritability. Of note, nonallelic interactions influencing the traits were detected by both scaling test and joint scaling test, indicating the inadequacy of the additive–dominance model alone in explaining the manifestation of complex traits such as yield. Besides, additive (*d*) and dominance (*h*) gene effects, different types of interallelic interactions (*i, j, l*) contributed towards the inheritance of traits in the given crosses. Nevertheless, predominance of additive variance suggests a difference between homozygotes at a locus with positive and negative alleles being distributed between the parents. Duplicate epistasis was prevalent in most of the cases for traits like plant height, seeds/pod, 100-seed weight and pod width. In view of the diverse gene actions, i.e. additive, dominant and epistasis, playing important roles in the manifestation of complex traits like yield, we advocate implementation of population improvement techniques in particular reciprocal recurrent selection to improve productivity gains in grass pea.

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Introduction

Grass pea (*Lathyrus sativus* L.) is a protein rich (27–29%) cool season legume crop belonging to family Leguminosae, used for human and animal consumptions since neolithic period (Campbell 1997; Hanbury *et al.* 2000) mainly in south Asian and African countries. In the past, it had got more attention as a hardy pulse crop adapted to extreme environmental situations like drought and rain-fed, where soil quality was poor, excessive rainfall or flooding along with resistance to a range of damaging pests (Kaul *et al.* 1986; Palmer *et al.* 1989; Campbell *et al.* 1994).

Presence of a very strong and deep penetrating root system enabled it to sustain on a wide range of soil types. Owing to its hardiness along with its ability to atmospheric nitrogen fixation, makes it an increasingly important pulse crop in changing environments, in particular, for the subsistence farmers. Despite the presence of several valuable attributes described above, the productivity gains have remained

unsatisfactory to a large extent and are attributable to the limited research efforts concentrated on yield improvement of this crop.

Grass pea is predominantly a self-pollinated crop with up to 28% cross pollination (Rahman *et al.* 1995). However, in breeding programme, it has been handled as a self-pollinated crop with majority of the selections focussing on single plant or pedigree method. Grain yield is a complex character and is the multiplicative end product of many yield components. Therefore, to attain the actual yield potential, the fundamental understanding of the genetics and inheritance that underlies the yield and its component characters are urgently required. Hence, adopting appropriate breeding and selection strategies for targeted trait improvement largely depend on the knowledge of gene action/effects operating in a particular breeding population. Nevertheless, the effect of various individual genes must be considered together with suitable statistical tools to maximize the derived genetic information. For any efficient breeding programme, information about nature and magnitude of gene action is required to accelerate the success rate (Shashikumar *et al.* 2010). The genes

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may exhibit additive, dominance and/or interaction effects. Information concerning the nature of gene action on complex traits such as yield and its contributing traits in grass pea is very less. Yield and its component characters indeed are quantitative in nature and are influenced by all three types of gene actions (Dixit 1998a, b; Saxena 2008). Therefore, it becomes imperative to test the significance of additive–dominance model for a trait so that the relationship could be established between generations.

The present investigation aims to elucidate the gene action associated with various yield attributes through generation mean analysis (GMA). Also, we estimated various kinds of gene effects and heritability through standard biometrical and statistical procedures.

Materials and methods

Plant material and experimental design

The experiment was conducted at main research farm of Indian Institute of Pulses Research (IIPR), Kanpur, India. The experimental material comprised of six generations including parents (P_1 , P_2), F_1 , F_2 , B_1 and B_2 , from three crosses of grass pea, namely, BioL-212 \times Prateek, BioL-212 \times Mahateora and Prateek \times BioL-208. The crossing programme to generate F_1 's was carried out during winter season of 2010–11, and raising of F_1 's to develop F_2 and back-cross progenies (B_1 and B_2) was done during winter season of 2011–12. To obtain sufficient F_1 seeds, the hybridization was conducted under insect proof nylon net, which in turn prevented natural out crossing. The evaluation trial of above said six generations (P_1 , P_2 , F_1 , F_2 , B_1 and B_2) were organized in the open field conditions during winter 2012–13 in a completely randomized block design with three replications. Each generation was planted in plot of 4 m length with row to row and plant to plant spacings of 30 and 10 cm, respectively. Parents and F_1 's were raised in two rows each; B_1 and B_2 of two rows each, while each F_2 was grown in a plot of four rows.

GMA

GMA was performed as proposed by Hayman (1958) involving two consecutive steps: (i) to detect presence or absence of nonallelic interaction (epistasis) and (ii) to estimate gene effects, variances and type of epistasis involved in trait inheritance. Further, adequacy of simple additive–dominance model was checked using scaling tests A, B, C and D as described by Hayman and Mather (1955) and Mather and Jinks (1971). The means of different generations were utilized to calculate the above said scales. The variances of A, B, C and D scales, namely V_A , V_B , V_C and V_D were computed by utilizing the variance of different generations (VP_1 , VP_2 , VF_1 , VF_2 , VB_1 and VB_2). The standard error of A, B, C and D was made by taking square root of respective variances of V_A , V_B , V_C and V_D and used for testing the

significance of the deviations of the respective scales from zero. To test the significance of the scales, student 't' test was used for each scale. The significance of the scales was examined using calculated P values for respective calculated 't' values.

Joint scaling test

Sometimes, Mather's scaling test remains inadequate to fully explain the additive–dominance model (Shahid 1996; Deb and Khaleque 2009). Hence, joint scaling test (Cavalli 1952) was undertaken which integrates multiple scaling tests and to test the competence of simple additive–dominance model or to detect epistasis for all the measured traits using χ^2 test.

Estimation of gene effects through six generations means

In a situation, where χ^2 and/or scaling tests, i.e. the simple additive–dominance model is inadequate, six parameter model or digenic interaction model based on Hayman's (1958) approach was used to separate the components of genetic variance to its main effects and to provide information on the inheritance of various characters. Assuming that the absence of both linkage and higher order gene interactions, the mean of generations were used to estimate gene effects or six genetic parameters, namely, m , d , h , i , j and l of digenic interaction. These parameters represent mean effect (m), genetic effects including additive (d) and dominance (h), and gene interaction effects comprising additive \times additive (i), additive \times dominance (j) and dominance \times dominance (l). The square roots of respective variances were used for the computation of standard error which were used to calculate the 't' values for testing significance of the corresponding gene effects.

Estimation of component of variance and heritability for different characters

The estimation of phenotypic (V_P), environmental (V_E), genotypic (V_G), additive (V_A) and dominance (V_D) variances from six generations variances were calculated according to the formulae given by Warner (1952) and Wright (1968). These estimates were obtained by using corresponding generation variances. Further, the heritability in broad sense (h^2b) was computed according to Mather (1949).

Results and discussion

To ascertain the nature of gene action for yield and its contributing traits, GMA was conducted using the data recorded on six generations of three grass pea crosses. The mean performance of the six generations including P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 for 10 traits is represented in table 1. The values of individual scaling tests and estimates of gene effects namely, m , d , h , i , j and l for different traits in these crosses were estimated (tables 2 and 3). The information on given estimates

Table 1. Scaling and joint scaling test (χ^2) for 10 yield contributing traits in three crosses of grass pea.

Scaling test factors	Plant height	Primary branches	Pods per plant	Seed per pod	100-seed weight	Pod length	Pod width	Biological yield per plant	Seed yield per plant	Harvest index
First cross (BioL-212 × Prateek)										
A	0.50	—	11.00	-0.40*	0.40*	0.29*	-0.02	9.70*	5.05**	10.23**
B	91.50*	5.00	29.50**	0.60	1.15*	0.76**	0.02	18.90**	4.70**	-2.34
C	-4.00	10.00	73.50**	1.00*	-3.15**	1.11**	0.24**	42.50**	11.45**	8.24
D	-48.00*	2.50	16.50*	0.40	-2.35**	0.030	0.12*	6.95	0.85	0.17
χ^2	24.88**	—	73.90**	32.10**	153.21**	146.98**	42.42	45.34**	60.46**	35.03**
Second cross (BioL-212 × Mahateora)										
A	-65.50**	2.50**	7.00	0.80*	-1.80**	0.38**	0.19**	-3.20	4.70**	31.79**
B	-58.50**	0.50**	-6.00	-2.30**	-0.90	-0.89**	-0.25**	0.30	-5.25**	-33.53**
C	19.00	-1.00**	39.00**	0.30	-2.20**	-0.29**	0.00	-3.90	-2.40*	-9.27
D	71.50**	-2.00**	19.00**	0.50**	0.25	0.11	0.03	-0.50	-0.95	-3.76
χ^2	417.60**	—	159.64**	127.36**	106.53**	925.98**	290.17**	3.06	146.85**	376.37**
Third cross (Prateek × BioL-208)										
A	0.50	—	11.00	-0.40*	0.40*	0.29*	-0.02	9.70*	5.05**	10.23**
B	46.50**	2.00*	-6.50**	0.20	-0.65	1.32**	0.14**	14.10**	0.90*	-14.03**
C	-4.00	10.00**	73.50**	1.00*	-3.15**	1.11**	0.24**	42.50**	11.45**	8.24
D	-25.50**	4.00**	34.50**	0.60**	-1.45**	-0.25**	0.06*	9.35	2.75*	6.02*
χ^2	43.48**	—	61.47**	35.91**	101.86**	543.41**	94.00**	83.32**	44.06**	48.10**

* $P < 0.05$ and ** $P < 0.01$.

in genetic architecture of the various traits are essential for judicious selection of parents and breeding methodology.

Adequacy of the genetic model

The data presented in table 2 shows that all the scaling tests, namely, A, B, C and D were insignificant for primary branches in first cross. Similarly, second cross also depicted nonsignificant joint scaling test for biological yield per plant. Based on the insignificance of the scaling tests (A, B, C and D), we proceeded for joint scaling test to accommodate the data within three parameter model to evaluate adequacy of simple additive–dominance model (Cavali 1952). χ^2 test was conducted to assess the goodness of fit of this model. χ^2 values were nonsignificant for primary branches and biological yield per plant in first cross and second cross, respectively, indicating the absence of digenic nonallelic interaction in these cases. In other two crosses, the data did not fit to joint scaling test. It indicated that additive–dominance model is adequate enough to explain the effects. The adequacy of simple additive–dominance model suggests that nonallelic interaction (epistasis) is absent and generation means depend only on additive–dominance effect of the gene. In general, such cases are usually dealt with the genetic model of Jinks and Jones. On the other hand, significance of one or more scaling tests, i.e. A, B, C and D for the remaining traits and crosses revealed the presence of epistasis in these traits and crosses (table 1). Therefore, well-defined experimental evidence supported the shortfall of the simple additive–dominance model for addressing the traits considered here. Of the 10 traits, nine in three crosses witnessed similar trends of significantly positive nonallelic interaction for one or more of the scaling tests. Further, six parameters model was used to estimate the type of gene effects for these traits. The results obtained here remain in close agreement with earlier published report (Sharma and Rastogi 2001).

Gene action and epistasis effects

In the present study, scaling test (Mather 1949) and joint scaling test (Cavali 1952) were found to be significant for most of the traits. This indicates that higher order interaction (interallelic interactions) plays an important role in the expression of a trait, and additive–dominance alone will not be sufficient to deal with such traits (Shahid 1996). In such conditions, available populations have to be forwarded to next generations to arrive at the best fit model (Mather and Jinks 1982). Digenic nonallelic interaction model with six parameters, namely *m*, *d*, *h*, *i*, *j* and *l* (Hayman 1958) portrayed that the epistatic interaction model sufficiently explained the gene action in the most of the studied traits. The result revealed (table 2) that mean effect of F₂ performance (*m*) was highly significant for all the studied traits in three crosses. Initially, it was noted that these characters were quantitatively inherited. In first cross (BioL-212 × Prateek), dominance (*h*) and dominance × dominance (*l*) gene effects

Table 2. Estimations of gene effects and epistasis for yield and its attributes in three crosses of grass pea based on six generation means (Hayman 1958).

Gene action	Plant height	Primary branches	Pods per plant	Seed per pod	100-seed weight	Pod length	Pod width	Biological yield per plant	Seed yield per plant	Harvest index
First cross (BioL-212 × Prateek)										
<i>m</i>	79.00**	6.50**	44.50**	3.10**	7.50**	2.64**	0.95**	25.45**	7.40**	32.22**
<i>d</i>	-50.00**	-2.50**	-4.50	-0.20	-0.95**	0.03	-0.02	-2.05	1.45	9.07**
<i>h</i>	91.00**	-5.00**	-45.25**	-0.50	4.42**	-0.48**	-0.24**	-19.05	-3.77	-3.47
<i>l</i>	-188.00**	-	-7.50	0.60	-6.25**	-0.99**	0.24*	-14.70	-8.05*	-7.55
<i>i</i>	96.00**	-5.00**	-33.00*	-0.80	4.70**	-0.06	-0.24**	-13.90	-1.70	-0.34
<i>j</i>	-45.50	-2.50	-9.25	-0.50	-0.37	-0.23	-0.02	-4.60	0.17	6.29
Epistasis	D	-	C	D	D	C	D	C	C	C
Second cross (BioL-212 × Mahateora)										
<i>m</i>	112.0**	4.00**	35.50**	3.10**	9.00**	2.75**	0.93**	14.90**	5.10**	33.98**
<i>d</i>	12.50**	2.00**	14.00**	1.20**	-0.65	0.43**	0.19**	1.30	3.95**	21.79**
<i>h</i>	-152.50**	1.50*	-48.50**	-1.55**	-0.10	-0.20	-0.06	-7.15**	-1.30	3.22
<i>l</i>	267.00**	-7.00**	37.00**	2.70**	3.20*	0.73**	0.12	1.90	-1.40	-5.79
<i>i</i>	-143.00**	4.00**	-38.00**	-1.20**	-0.50	-0.22	-0.06	1.00	1.90	7.53
<i>j</i>	-3.50	1.00	6.50	1.55	-0.45	0.63	0.22	-1.75	5.00	32.66
Epistasis	D	D	D	D	D	D	D	D	C	D
Third cross (Prateek × BioL-208)										
<i>m</i>	79.00**	6.50**	44.50**	3.10**	7.50**	2.64**	0.95**	25.45**	7.40**	32.22**
<i>d</i>	-27.50**	-1.00*	13.50**	-	-0.05	-0.25**	-0.08**	0.35	3.35**	14.92**
<i>h</i>	46.00**	-8.00**	-81.25**	-0.90*	2.62**	0.07	-0.12**	-23.85*	-7.57**	-15.17**
<i>l</i>	-98.00**	6.00*	64.50**	1.40*	-2.65**	-2.11**	0.00	-5.10	-0.45	15.83
<i>i</i>	51.00**	-8.00**	-69.00**	-1.20**	2.90**	0.50**	-0.12**	-18.70	-5.50*	-12.04*
<i>j</i>	-23.00	-1.00	8.75	-0.30	0.52	-0.51	-0.08	-2.20	2.07	12.13
Epistasis	D	D	D	D	D	D	D	C	C	D

m, Mean; *d*, additive; *h*, dominance; *l*, dom × dom; *i*, add × add; *j*, add × dom. **P* < 0.05 and ***P* < 0.01.

Table 3. Summarized table of different gene interactions for 10 yield contributing traits in three crosses of grass pea.

Gene action	Plant height	Primary branches	Pods per plant	Seed per pod	100-seed weight	Pod length	Pod width	Biological yield per plant	Seed yield per plant	Harvest index
Mean (<i>m</i>)	**	**	**	**	**	**	**	**	**	**
Additive (<i>d</i>)	**	**	**	-	*	*	*	-	*	**
Dominance (<i>h</i>)	**	**	**	*	*	*	*	*	-	-
Dom × dom (<i>l</i>)	**	*	**	*	*	**	-	-	-	-
Add × add (<i>i</i>)	**	**	**	**	*	-	*	-	-	-
Add × dom (<i>j</i>)	-	-	-	-	-	-	-	-	-	-

P* < 0.05 and *P* < 0.01.

displayed opposite signs for the traits, namely, plant height, seeds per pod, 100-seed weight and pod width indicating duplicate epistasis. The values of dominance (*h*) and dominance × dominance (*l*) interaction were in the same direction for traits like pods per plant, pod length, biological yield per plant, seed yield per plant and harvest index and the interaction followed the complementary mode of nonallelic gene interaction. Presence of complementary gene action for above mentioned traits indicates that parents selected for crossing are diverse. Therefore, it is possible to realize enhanced genetic gain in breeding programme. In the present investigation, genotypes BioL-212 and Prateek could be identified as the best parents since their respective crosses showed complementary gene action for seed yield per plant and biological yield per plant. These findings are in accordance with a report published recently in pigeonpea (Ajay *et al.* 2012).

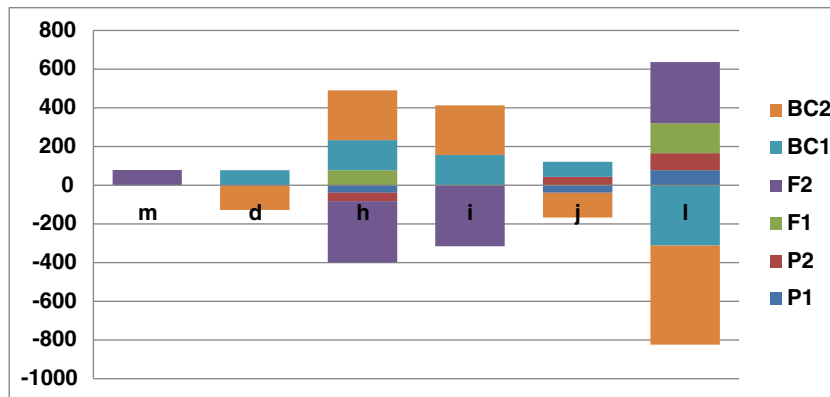
The classification of gene interaction depends on the magnitude and sign of the estimates of dominance (*h*) and dominance × dominance (*l*) effects, when there are many pairs of interacting genes (Mather and Jinks 1982). The sign associated with the estimates of additive effects (*d*) and dominance effects (*h*) indicates the parent who concentrates the highest number of genes or positive alleles for increasing the traits (Falconer). Therefore, the significant but positive *d* for harvest index indicates that additive effect of the gene is predominant and selection for this trait should be delayed to later generations. The significant negative value of *d* for other traits indicated that the inheritance of these traits is not controlled by additive gene action. Similarly, the significant and positive value of *h* for plant height and 100-seed weight showed that the dominant effect of gene is predominant. Presence of *h* indicates that selection should be delayed until heterozygosity is reduced in population. The earlier finding reported that traits with high magnitude of dominance than additive can be improved through conventional breeding approach such as pedigree or bulk or single seed descent method if selection is delayed until later generation when the dominance effect would have diminished (Sirohi and Gupta 1993). On the contrary, the significant but negative values of *h*, *i*, *j* and *l* for some traits showed that negative alleles were also dispersed in the parents involved in the cross. Negative sign of *h* in cross for any trait indicates that dominance effects were contributed by the parents having alleles responsible for low value for the traits, for example, in plant heights of BioL-212, Mahateora and Prateek in respective crosses. Thus, selection for these traits should also be delayed to later generation when desirable segregants become available. The significant but similar sign of *d* and *h* for primary branches indicated predominant role of additive and dominant effects for the inheritance of these traits. The type of epistatic interaction additive × additive (*i*) was significant for plant height in first and third crosses. Additive × dominance type of epistasis (*j*) was nonsignificant with negative sign for all traits in all crosses, which indicate that this type of epistasis is not contributing in inheritance of any trait in the crosses. The *d* effect for biological yield per plant, seed yield per plant,

Pods per plant, pod length and pod width was nonsignificant indicating involvement of several genes with small effects.

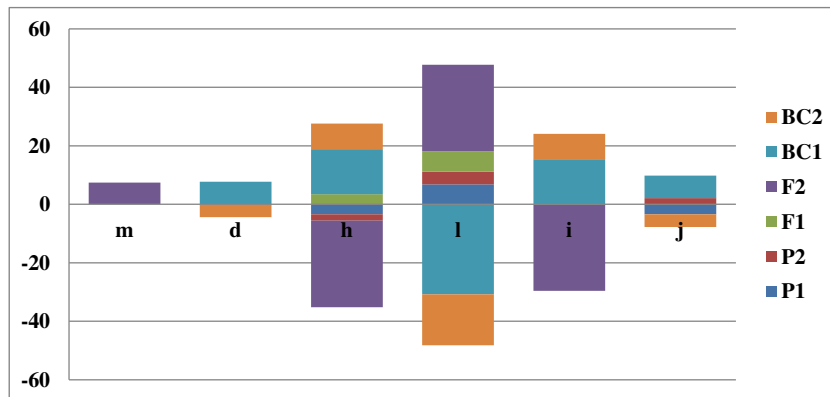
In second cross (BioL-212 × Mahateora), dominance (h) and dominance × dominance (l) gene effects displayed opposite signs for all the traits except seed yield per plant witnessed duplicate epistasis. The opposite signs of h and l counterbalance each other, thus leading to reduced heterosis (Shashikumar et al. 2010). The positive sign of additive effects (d) for all the traits except 100-seed weight indicates that the additive effect of gene is predominant for all traits, and 100-seed weight exhibited negative value of d suggest that these traits are not controlled by additive gene action. In case if magnitude of d was less, then we could move for heterosis breeding. The estimates of h , i and l were found significant with negative signs suggesting that selection for the traits, namely, plant height, primary branches, pods per plant, seed per pod, biological yield per plant should be delayed to later generation, so that negative alleles are removed. Hence, improvement of these traits could be achieved through recurrent selection procedure (Singh and Narayanan 2000). The significant but similar signs of d and h for primary branches in all crosses indicated predominant role of additive and dominant effects for the inheritance of this trait. Both

additive and nonadditive gene effects were also reported in earlier studies (Joseph and Kumar 2000). Nonsignificant d effects for biological yield per plant and 100-seed weight indicates that these traits are under the control of several genes (Dixit 1998b; Ajay et al. 2012).

Third cross (Prateek × BioL-208) showed opposite sign for dominance (h) and dominance × dominance (l) type of interaction for all the traits except biological yield per plant and seed yield per plant. It indicates that all the traits depicted duplicate type of epistasis and biological yield per plant and seed yield per plant displayed complementary type of epistatic effect. The complementary type suggested the possibility of considerable amount of heterosis for these two traits in this particular cross (Punia et al. 2011). Duplicate type of nonallelic gene interaction for most of studied traits with few exceptions further confirms the prevalence of dominance effects (Singh and Sharma 2001). Presence of duplicate epistasis indicates that variability in segregating generations may be reduced which hinder the selection process (Kumar and Patra 2010), hence it is difficult to utilize them in breeding programme (Sameer et al. 2009). The positive sign of additive effect (d) for seed yield per plant and harvest index indicated that these traits are



(a)



(b)

Figure 1. Relative contributions of different types of gene effects (additive/dominance) and interactions (epistasis) for (a) plant height and (b) seed yield per plant. The parameters are calculated by recording trait-measurements on parents, derived F₁ and generations which are shown by different colours.

Table 4. Estimations of variances components for 10 yield contributing traits in three crosses of grasspea.

Genetic components of variation	Plant height	Primary branches	Pods per plant	Seed per pod	100-seed weight	Pod length	Pod width	Biological yield per plant	Seed yield per plant	Harvest index
First cross (BioL-212 × Prateek)										
V_G	7.14	1.95	269.32	0.17	-0.49	-0.02	-0.001	173.32	6.511	15.06
V_A	-806.62	3.26	426.33	0.11	-0.08	0.03	-0.002	265.80	6.75	76.41
V_D	813.77	-1.30	-157.00	0.05	-0.41	-0.06	0.002	-92.48	-0.23	-61.35
V_P	37.24	2.32	281.63	0.25	0.09	0.02	0.003	173.48	6.99	39.49
h^2_b	0.192	-	0.95	0.65	-5.30	-1.26	0.000	0.99	0.93	0.38
Second cross (BioL-212 × Mahateora)										
V_G	-366.55	-0.185	-21.65	-0.14	-0.16	0.009	-0.002	-16.97	-0.879	2.78
V_A	-10.23	-1.11	-53.12	-0.03	-1.03	-0.015	-0.001	-3.26	-3.949	-59.34
V_D	-356.31	0.926	31.46	-0.11	0.86	0.024	0.000	-13.70	3.070	62.12
V_P	37.24	0.00	2.32	0.09	0.04	0.013	0.001	0.838	0.838	16.44
H^2_b	-9.84	-9.84	-9.30	-1.58	-4.08	0.710	-1.745	-20.26	-1.049	0.169
Third cross (Prateek × BioL-208)										
V_G	7.14	-1.95	269.32	0.170	-0.494	-0.026	-0.001	173.32	6.511	15.06
V_A	-58.01	2.43	472.99	-	0.072	0.036	0.004	304.03	8.950	54.81
V_D	65.16	-0.47	-203.67	-0.303	-0.566	-0.062	-0.005	130.71	-2.439	-39.75
V_P	37.24	2.32	281.63	0.259	0.093	0.020	0.003	173.48	6.993	39.49
h^2_b	0.192	-	0.956	0.656	-5.305	-1.261	-	0.999	0.931	0.381

V_G , genotypic variance; V_A , additive variance; V_D , dominance variance; V_P , phenotypic variance; h^2_b , heritability in broad sense.

governed by additive effect of genes. Significant but negative value of d for most of the traits indicated that the inheritance of these traits in this particular cross combination is not controlled by additive genes. The significant but similar sign of d and h for primary branches and pod width indicated predominant role of additive and dominant effect for the inheritance of these traits. In this cross biological yield per plant and 100-seed weight lacked significant d effects indicated that these traits are under the control of complex gene pathway in this cross involving several minor genes with small effect and different expressions (Mathews *et al.* 2008). The estimates of h and l were found significant with positive sign for some traits indicated predominant role of dominant component in the inheritance of these traits. Significant but positive sign of i (additive \times additive) for any of the traits portrayed that the inheritance of these traits in a particular cross is controlled by additive gene action. Overall additive gene effects were exhibited in 19 of 30 cases (10 traits \times 3 crosses), however, the relative magnitude of these effects to the mean effects (m) suggests that they are of minor importance in the explanation of traits variation. The positive sign of additive effects (d) for seed yield per plant in second and third crosses indicated predominant role of additive gene action for the inheritance of this trait. All types of gene action effects (d , h and epistasis) were highly significant or significant, while dominance \times dominance component (l) gene effect also played a major role in the inheritance of the studied traits. Among the individual epistatic gene effects, additive \times additive (i) and dominance \times dominance (l) effects appear to contribute more to the performance of most traits and crosses than do the additive \times dominance (j) gene effect. These findings are in concordance to the earlier report in which significant l for most of the yield attributes in pigeonpea were observed (Hooda *et al.* 2003; Ajay *et al.* 2012). In all the crosses, though scaling test was significant but nonallelic interactions were not significant for some important traits like biological yield per plant, seed yield per plant and harvest index. This indicates that such traits are governed by higher order interactions or they are under the control of complex genetic control or they have larger environmental variance (Milus and Line 1986). It has been observed that higher order epistasis among more than two genes may play crucial role in genetic interactions (Purcell *et al.* 2007; Imielinski and Belta 2008).

In summary, the additive (d) as well nonadditive gene actions (h , l , i) were important for plant height, primary branches and pods per plant, whereas for seed yield and harvest index, additive gene action was important. Further, seeds per pods, 100-seed weight and pod length were also controlled by both additive and nonadditive gene actions and biological yield per plant is mainly governed by dominance gene action (table 3). These findings are in congruence to earlier report on grass pea (Dixit 1998a, 1999). Relative contributions of gene effects and interactions towards manifestation of a particular trait are illustrated in figure 1 taking plant height and seed yield per plant as examples.

Components of variance

Variation estimation using values from six generations revealed that variation due to additive effect was predominant for most of the traits studied (table 4). Estimation of variance components in these six generation materials indicate that additive genetic variance was higher than the dominance variance for the traits under the study in first and third crosses. The predominance of additive gene action revealed that it is fixable in nature and selection for these traits will be very effective in such crosses. Selection is the reliable breeding method for improving character with predominant additive variance. Dominance variance was more pronounced in the inheritance of plant height. On the contrary, dominance variance was more prominent as compared to additive genetic variance in second cross. Here, the dominance variance is high and the selection has to be postponed to later generations (Ajay *et al.* 2012; Pathak *et al.* 2014). The dominance component was negative for different traits, namely, pods per plant, 100-seed weight, biological yield per plant, seed yield per plant, plant height, etc. in three crosses. In previous study, negative dominance effect has been reported in many crops like chickpea (Deb and Khaleque 2009), pigeonpea (Ajay *et al.* 2012) and melon (Zalapa *et al.* 2006). Mather (1949) had inferred that this negative value of dominance variances arises due to sampling error and/or genotypes and environmental interactions (Robinson *et al.* 1955). Hence, in the present investigation, both additive and dominance variances were playing important role in the inheritance of studied traits. This observation finds agreement with earlier published reports in which both additive and nonadditive gene effects were involved in the expression of many traits such as number of primary branches, pods per plant and grain yield per plant (Dixit 1998a, 1999; Parihar *et al.* 2015). Unlike here, plant height was found to be predominantly under the control of dominance gene effects (Dixit 1998a). The phenotypic variance component was higher than genotypic component for most of the studied traits across the crosses indicating predominance of environmental component of variance over the genotypic components of variances. Heritability was estimated only in broad sense among the three crosses (table 4). Highest broad sense heritability was exhibited by biological yield per plant, seed yield per plant and pods per plant in first and third crosses. In second cross, highest heritability depicted for pod length followed by harvest index. High heritability for above said traits indicates that these traits are likely amendable to genetic manipulation and selection may be rewarding for these traits (Dixit 1998a).

Conclusion

In any breeding programme, improving yield becomes the main breeding objective, and yield is a collective manifestation of several other component traits. Based on the present investigation, it could be inferred that yield and its contributing traits exhibited all three types of gene actions, i.e.

additive, dominant and epistasis. In such situation, recombination breeding could be used, followed by selection delayed to later generations. Therefore, improvement of such traits in grass pea may be expected through standard selection procedures, which may first exploit additive gene effects. Simultaneously, care should be taken that dominant gene effects are not removed, rather they should be concentrated. Predominance of additive variance suggests that there is difference between homozygotes at a locus with positive and negative alleles being distributed between parents. Owing to some crosspollination in grass pea, such type of interactions could be exploited by selection of individuals based on their performance in recurrent selection. Therefore, due to the presence of all gene actions, namely, additive, dominant and epistasis, reciprocal recurrent selection is the best suited strategy to meet the need of yield improvement. This procedure is equally effective for utilization of both additive and nonadditive gene effects. In case, where nonadditive effects hold considerable importance in trait expression, recurrent selection for specific combining ability can be used as a suitable breeding procedure. Although, the recurrent selection procedure is generally not used for improvement of completely selfpollinating crops, it can be effectively used in grass pea given the variable extent of crosspollination in this crop. Therefore, the recurrent selection that capitalizes all the three types of gene effects would certainly result in the recovery of desirable recombinants in advanced generations.

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