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ANALYSIS OF GENE EFFECTS FOR YIELD AND YIELD COMPONENT TRAITS IN FABA BEAN (*Vicia faba* L.) GENOTYPES

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ABSTRACT

The gene effects for yield and yield component traits in faba bean genotypes of indigenous and exotic origins were estimated using generation mean analysis of five generations (P_1 P_2 F_1 F_2 and F_3) in nine crosses for ten quantitative traits using two models. By five parameter model preponderance of additive and additive x additive interaction effects was observed with respect to days to maturity, plant height, branches per plant, clusters per plant, pod length, pods per plant and 100 seed weight while preponderance of dominance effect was observed in days to 50% flowering, seeds per pod and yield per plant. By joint scaling test preponderance of additive effects was observed for days to 50% flowering, days to maturity, plant height, clusters per plant, pods per plant and yield per plant and of dominance and dominance x dominance interaction effect with respect to branches per plant, pod length, seeds per pod and 100 seed weight. Duplicate epistasis was present in one cross each in plant height, pod length, seeds per pod and 100 seed weight, in two crosses each in days to 50% flowering, pods per plant and yield per plant and three crosses each in branches per plant and clusters per plant by five parameter model. However, duplicate epistasis was predominantly present in all the crosses for all the traits except a single cross each in days to 50% flowering, plant height, branches per plant and seeds per pod indicating that selection for improvement may be successful in later generations. It was concluded that the traits showing preponderance of fixable component of variance should be more responsive to selection than the traits with non-fixable component of variance and accordingly the preferable breeding strategy for faba bean improvement has been suggested.

Key words: Generation means, Gene effects, Five parameter model, Joint scaling test, *Vicia faba*

INTRODUCTION

Faba bean (*Vicia faba* L.) is world's seventh most produced legume crop, widely cultivated for human food, animal feed and fodder (Oliveira *et al.,* 2016). It is an annual, diploid (2n = 2x =12), self-compatible, autogamous plant, with average partial allogamy ranging from 32-40% (Bishnoi *et al.* 2012). It is one of the earliest domesticated plants, believed to be domesticated during the Neolithic period. The species *Vicia faba* is genetically isolated i.e. it does not cross with other species of the genus *Vicia* and thereby it does not allow gene exchange with any other species including its close relative *Vicia narbonensis*. Genetic variability in global faba bean germplasm is quite high which is attributed to its intermediate crossing system between autogamy and allogamy and wide geographic distribution (Negash *et al.,* 2015; Sharifi, 2015). Faba bean is one of the most efficient symbiotic atmospheric nitrogen fixer and ranks next only to soybean in terms of seed protein content which ranges from 20 to 40% in different genotypes and environments (Bishnoi, 2016). At present faba bean is cultivated in more than 50 countries of the world. The world production of faba bean was 3.4 million metric tons in the year 2013 (Landry *et al.* 2015). However, in India it has been categorized as an underutilized potential legume crop. It was introduced into India through Mesopotamia probably after the advent of the Arabian spice trade route which came in to existence around 3000 B.C. (Kumar *et al.* 2016). Although, the acrage and production data are not available but it is reported to be grown in sizeable areas in the states of Bihar, Madhya Pradesh and some part of Uttar Pradesh in India (Kumar *et al.* 2017). The yield potential remains unrealized in faba bean mainly due to lack of success in hybrid breeding for exploitation of heterosis. Therefore, improvement in seed yield and yield stability addressed through the component traits, resistance against lodging, drought, frost, fungi and other pathogens and pests as well as synchronous maturity and elimination of pod shattering are major breeding objectives in faba bean improvement. (Bishnoi *et al.* 2015). In this context the knowledge of magnitude and nature of the gene effects controlling different quantitative traits is very important. Various biometrical methods are available for investigation of the inheritance of quantitative traits which can predict the performance of the material before selection is actually practiced. Five parameter model as suggested by Hayman (1958) and joint scaling test as described by Cavalli (1952) are two such models. Five parameter model is used in the absence of the back cross data and it estimates not only additive and dominance effects but also various interactions as well. On the other hand joint scaling test is described as superior to other scaling tests as it provides estimates of genetic parameters along with the adequacy of the model if the number of generation mean is more than the number of parameters to be estimated. Further, the epistatic gene effects cannot be estimated by a conventional line x tester model. This limitation can also be overcome by employing five parameter model and joint scaling test. The knowledge about the mode of inheritance and nature and magnitude of gene effects is of considerable importance for developing high yielding varieties in faba bean (Beyene, 2015). Therefore, the objectives of the present study were to estimate different types of gene effects operating in the inheritance of yield and yield component traits in faba bean including the epistatic effects and to suggest a suitable breeding strategy for this very important legume crop.

MATERIALS AND METHODS

The experimental material consisted of 16 faba bean genotypes originating from India and abroad which were crossed in line x tester fashion to obtain 48 F_1 hybrids (Table 1). Out of these, nine promising crosses were selected on the basis of morphological variation, *per se* performance and other desirable attributes for generation mean analysis and estimation of gene effects (Table 2). The parents and their F_1, F_2 and F_3 progenies from the nine crosses were grown in *Rabi* 2013-14 and 2014-15 in randomized block design with three replications. A row length of 5 m was kept with an inter row distance of 45 cm. The interplant distance was kept 20 cm within the individual rows. The generation means of the five generations were computed from individual data as

$$\bar{X} = \frac{\sum x_i}{N}$$

Where

$\bar{X}$ =Generation mean

$\sum X_i$ =Grand total

n =Number of plants

The estimate of variance of a generation mean ($^V\bar{X}$) was obtained by dividing the variance within generation (^VX) by the total number of individuals in that generation.

$$^V\bar{X} = \frac{^VX}{n}$$

Where

$^V\bar{X}$ = Variance of generation mean

^VX = Variance among the individuals within generation

n = Number of individuals within generation

The means of parents and F_1, F_2, and F_3 generations were used for the estimation of five parameters viz., mean (m), additive effects (d), dominance effects (h), additive × additive interaction effects (i) and dominance × dominance interaction effects (l) in nine crosses following five parameter model of Hayman (1958) and Joint scaling test of Cavalli (1952) according to least square technique for ten quantitative characters. The standard errors were calculated by taking the square root of the variances. Since the number of estimated parameters was equal to the number of the generations used, no degree of freedom was left for testing the adequacy of the model. The genetic parameters were tested for their significance by 't' test. The type of epistasis whether complimentary or duplicate was determined by the signs of (h) and (l). The type of epistasis was interpreted as complimentary if h and l both had same signs and duplicate if they had opposite signs.

RESULTS AND DISCUSSION

The generation means and estimates of additive, dominance, additive x additive and dominance x dominance gene effects are presented in table 3a and 3b for five parameter model (Hayman, 1958) and in table 4a and 4b for joint scaling test (Cavalli, 1952).

By five parameter model the additive effect was significant in all the crosses except in HB-85 × HB-43, Vikrant × HB-43 and Vikrant × EC-117705 while the dominance effect was significant except in HB-85 × HB-43 for number of days to 50% flowering. The additive × additive interaction was significant except in HB-85 × HB-43 and HB-(M)-1 × EC-117705 and dominance × dominance interaction was significant except in HB-85 × HB-43 and Vikrant × HB-43.The epistasis was of complimentary type except in HB-(M)-1 × EC-117705 and Vikrant × HB-43 in which it was of duplicate type. All effects estimated by five parameter model were significant for number of days to maturity except dominance effect in HB-(M)-1 × EC-117705. The epistasis was of duplicate type in three crosses and of complementary type in the rest of them. For plant height all effects were significant except dominance effect in HB-86 × HB-8 by five parameter model and the epistasis was of duplicate type in only one cross. All effects were significant for number of branches per plant by five parameter model except additive effect in Vikrant × EC-621829, dominance in HB-86 × EC-117705 and additive x additive in HB-86 × HB-8 and Vikrant × HB-43. Duplicate epistasis was observed in three of the crosses. For number of clusters per plant by five parameter model all effects were significant except additive effect in HB-86 × EC-117705 and dominance effect in HB-86 x EC-117705 and HB-(M)-1 x HB-43. Duplicate epistasis was observed in three of the crosses. All effects were significant except additive effect in Vikrant × EC-117705 and dominance x dominance in Vikrant x HB-43 for pod length and duplicate epistasis was present in a single cross only. For number of pods per plant by five parameter model, additive effects were significant except in HB-85 × HB-43, HB-85 × EC-117705 and HB-86 × EC-117705 and dominance effect was significant except in a single cross HB-(M)-1 x EC-117705. Two of the crosses showed presence of duplicate type of epistasis. For the trait number of seeds per pod, additive effect was significant except in HB-85 × HB-43, HB-85 × EC-117705, Vikrant x HB-43, Vikrant x EC-117705 and Vikrant × EC-621829 and dominance effect was significant in all the cross except HB-86 x EC-117705. Duplicate epistasis was present in a single cross. For 100 seed weight by five parameter model additive effects were significant except in HB-(M)-1 × EC-117705 and Vikrant x HB-43 and only a single cross exhibited duplicate type of epistasis. All effects were significant for seed yield per plant by five parameter model except additive effects in three crosses viz. Vikrant x HB-43, Vikrant x EC-117705 and Vikrant x EC-621829. Duplicate type of epistasis was present in two of the crosses. By joint scaling test all the effects were significant except additive × additive interaction effect in HB-85 × EC-117705, HB-86 × HB-8, HB-(M)-1 × HB-43, Vikrant × HB-43 and Vikrant × EC-621829 and dominance × dominance interaction effect in HB-(M)-1× EC-117705.The epistasis was of duplicate type in all the crosses except in one cross where epistatic effects were not present. For days to maturity, the additive effect estimated by joint scaling test was non-significant in the cross HB-86 × HB-8, dominance effect in HB-(M)-1 × EC-117705and additive × additive interaction in HB-(M)-1 × HB-43 and Vikrant × EC-621829. Duplicate epistasis was present in all the crosses except one cross in which epistatic effects were not present.

For plant height all effects except additive × additive interaction effect in HB-86 × HB-8 and Vikrant × EC-621829 were significant. and The epistasis was of complimentary type in a single cross.. For number of branches per plant, additive effects were significant only for HB-85 x EC-117705 and HB-(M)-1× EC-117705 while dominance effect was non-significant only in a single cross viz. Vikrant x HB-43. The additive x additive interaction effect was significant in HB-86 x HB-8, HB-86 x EC-117705, Vikrant x EC-117705 and Vikrant x EC-621829 and dominance x dominance interaction effect was non-significant only in two crosses viz. HB-86 x HB-8 and Vikrant x HB-43. Duplicate epistasis was observed in all but one cross.

The additive effect in HB-85 × EC-117705, HB-86 × EC-117705 and Vikrant × EC-621829, dominance effect in HB-85 × EC-117705, additive x additive in HB-85 x HB-43 and Vikrant x HB-43 and dominance x dominance in Vikrant x HB-43 were non-significant for number of clusters per plant and the epistasis was of duplicate type in all the crosses.

The additive effects were significant only in two crosses HB-85 × HB-43 and HB-85 × EC-117705 and dominance effect was significant except in a single cross Vikrant x HB-43 for pod length.. The additive x additive interaction effect was significant only for two crosses viz. HB-86 X HB-8 and HB-86 X EC-117705 while dominance x dominance interaction effect was significant for all the crosses. The epistasis was of duplicate type in all the crosses.

For number of pods per plant, all effects were significant and all the crosses exhibited duplicate type of epistasis.

The additive effect was significant only in HB-86 X EC-117705 and Vikrant x EC-117705 and dominance effect was significant except in HB-86 × HB-8,HB-86 × EC-117705, HB-(M)-1 x EC-117705, Vikrant x HB-43 and Vikrant × EC-621829 for number of seeds per pod. The additive × additive interaction was non-significant for all the crosses and dominance x dominance interaction was significant only for HB-85 x HB-43, HB-85 × EC-117705, HB-(M)-1 × HB-43 and Vikrant × EC-117705. Complimentary epistasis was present in a single cross.

For 100 seed weight, the additive effects were significant except in HB-85 × EC-117705, HB-86 × EC-117705, HB-(M)-1 × HB-43, HB-(M)-1 × EC-117705 and Vikrant × EC-117705 while additive × additive interaction was non-significant in HB-85 × EC-117705and Vikrant × EC-621829 and all the crosses exhibited duplicate type of epistasis.

The additive effect was significant except in two crosses viz. Vikrant x HB-43 and Vikrant x EC-117705 for seed yield per plant and the epistasis was of duplicate type in all the crosses.

The gene effects estimated by both five parameter and joint scaling test for all nine crosses revealed the preponderance of additive and additive × additive gene effects for plant height, preponderance of dominance and dominance × dominance gene effects for number of branches per plant, number of pod clusters per plant, number of seeds per pod and 100 seed weight and additive, dominance, additive × additive and dominance × dominance gene effects in number of days to 50% flowering, number of days to maturity, pod length, number of pods per plant and seed yield. Duplicate epistasis by five parameter model was present for plant height, number of days to 50% flowering, number of clusters per plant, number of pods per plant in a single cross each, while for seed yield per plant duplicate epistasis was present in two crosses. Complimentary epistasis by Joint scaling test was present in plant height, number of branches per plant and number of seeds per pod. These results are in agreement with Bakhit and Abdel-Fatah, (2013) who reported that additive gene effects were significant for all the studied characters in faba bean except for seed yield per plant. The presence of significant additive effects in number of days to flowering, number of days to maturity, seed yield and number of pods per plant and additive × additive interactions for number of days to maturity, plant height, number of pods per plant, 100 seed weight and seed yield is in agreement with the results previously reported by Al-Fahady, (2009). Al-Fahady, (2009) also reported significant dominance × dominance interactions for number of days to flowering and seed yield per plant, which supports the findings of the present study. The digenic interaction types, additive x additive (i) and dominance x dominance (l) were significant in most cases with some exceptions which was supported by the findings of El-Deeb *et al.*(2008). However, the results of the present study are in contrary to Schill *et al.* (1998) who reported that dominance effects and additive × additive epistasis for yield was not significant. The additive × additive and dominance × dominance components of the epistatic interactions were significant for plant height, number of branches per plant and seed yield per plant in the present study which is in agreement with El-Deeb *et al.* (2008). Khodambashi (2012) reported that additive, dominance and at least one of the epistatic effect i.e. additive × additive and dominance × dominance were involved in the inheritance of seed yield per plant, plant height, pod length, 100-seed weight, number of pods per plant, primary branches, clusters per plant, nodes per main stem, secondary branches, and the number of seeds per pod in lentil, which supports the findings of the present study. The importance of additive as well as non-additive gene effects with predominance of non-additive gene effects in inheritance of seed yield and yield components in pigeonpea were reported by Vaghela *et al.,* 2009; Shoba and Balan, 2010 and Pandey *et al.,* 2013, which are in agreement with the present study.The predominance of non-fixable gene effects and presence of duplicate epistasis in yield indicated that maintenance of heterozygosity would be useful for yield enhancement in faba bean and therefore, selection should be effective at later generations. Hence, the breeding strategy for attaining high yield in faba bean would be the full or partial exploitation of heterosis through development of hybrids, synthetics or composite cultivars by facilitating open pollination mediated by insects particularly the honeybees. However the open pollinated varieties may pose a problem in the national variety identification system due to lack of uniformity. Therefore, the ultimate breeding strategy for high yield and uniformity of produce would be the development of hybrids which are currently limited by the lack of a stable CMS system in faba bean.

Table 1. The parental genotypes, their source and characteristic features.

S.No	Genotype	Origin/Source	Characteristic features
1.	HB-8	CCSHAU, Hisar	Medium maturity, tall plants, small seed size, medium yield, sensitive to lodging, less pod shattering at maturity, More number of seeds per pod.
2.	HB-14	CCSHAU, Hisar	Early maturing, long pods, more number of seeds per pod, bold seed, pod shattering at maturity.
3.	HB-23	CCSHAU, Hisar	Medium maturity and plant height, medium seed size, pod shattering at maturity, low yield.
4.	HB-36	CCSHAU, Hisar	Medium to late maturity, medium to longer plant height, small seeds, longer pods, medium yield, less pod shattering, highly resistant to diseases.
5.	HB-43	CCSHAU, Hisar	Profuse branching, more number of pod clusters, profuse podding, medium to large seed size, less pod shattering, resistant to diseases and high yield.
6.	HB-46	CCSHAU, Hisar	Medium maturity, medium to short plants, high pod shattering, asynchronous maturity, medium seed size and yield.
7.	HB-49	CCSHAU, Hisar	Early maturing, moderately tolerant to lodging, profuse branching, more number of pod clusters, profuse podding High yield.
8.	HB-85	CCSHAU, Hisar	Early maturing, profuse podding, higher number of seeds per pod, bold seeds, high yielder, synchronous maturity, medium pod shattering.
9.	HB-86	CCSHAU, Hisar	Higher number of seeds per pod, medium to bold seed size, medium yield, high pod shattering.
10.	HB-(M)-1	CCSHAU, Hisar	Long pods, more number of seeds per pod, bold seed, high yielder, more pod shattering, different leaflet shape and size.
11.	Vikrant	CCSHAU, Hisar	Released variety, medium seed size, medium yield, resistant to diseases and salinity, low pod shattering.
12.	EC-117705	NBPGR New Delhi	Profuse branching, more number of pod clusters, profuse podding, bold seed, high yielder, asynchronous maturity
13.	EC-	NBPGR	Late maturing, medium height, moderately sensitive to lodging, small seed

	321682	New Delhi	size, low yield.
14.	EC-247640	NBPGR New Delhi	Medium maturity, small plants, tolerant to lodging, bold seeds, tolerance to pod shattering, low yield.
15.	EC-591864	NBPGR New Delhi	Tolerant to lodging, profuse branching Longer pods, bold seed, asynchronous maturity, high pod shattering, lower to medium yield.
16.	EC-628938	NBPGR New Delhi	Late maturity, low plant height, tolerant to lodging longer pods, synchronous maturity, sensitive to diseases, medium seed size and low yield.

Table 2. The list of nine crosses used for generation mean analysis

S.No.	Cross
1	HB-85×HB-43
2	HB-85×EC-117705
3	HB-86×HB-8
4	HB86×EC-117705
5	HB-(M)-1×HB-43
6	HB-(M)-1×EC-117705
7	Vikrant×EC-628938
8	Vikrant× EC-117705
9	Vikrant×HB-43

Table 3 a. Gene effects estimated by five parameter model (Hayman, 1958).

	Cross	m	d	h	i	l	Epistasis
	Days to 50%flowering						
1	HB-85 × HB-43	73.00^{**}	-4.67^{**}	18.00^{**}	-114.67^{**}	14.67^{**}	C
2	HB-85 × EC-117705	52.00^{**}	-5.17^{**}	-17.56^{**}	36.44^{**}	-19.39^{**}	C
3	HB-86 × HB-8	65.67^{**}	-2.50^{**}	2.00^{**}	-50.67^{**}	3.50^{**}	C
4	HB-86 × EC-117705	65.00^{**}	-3.83^{**}	4.00^{**}	-58.67^{**}	7.83^{**}	C
5	HB-(M)-1×HB-43	74.33^{**}	2.33^{**}	4.00^{**}	-69.33^{**}	19.00^{**}	C
6	HB-(M)-1 × EC-117705	65.00^{**}	2.33^{**}	-6.00^{**}	2.67	4.00^{**}	D
7	Vikrant × HB-43	57.33^{**}	-0.17	-11.33^{**}	8.00^{*}	0.5	D
8	Vikrant × EC-117705	69.67^{**}	0	5.56^{**}	-57.78^{**}	11.89^{**}	C
9	Vikrant × EC-621829	76.00^{**}	-3.67^{**}	9.11^{**}	-75.56^{**}	9.44^{**}	C
	Days to maturity						
1	HB-85 × HB-43	174.33^{**}	-1.17^{**}	16.89^{**}	-108.44^{**}	21.06^{**}	C
2	HB-85 × EC-117705	144.33^{**}	4.83^{**}	-29.33^{**}	69.33^{**}	-8.17^{**}	C
3	HB-86 × HB-8	168.00^{**}	-1.50^{**}	6.44^{**}	-70.22^{**}	11.28^{**}	C
4	HB-86 × EC-117705	170.00^{**}	1.33^{*}	9.78^{**}	-99.56^{**}	22.78^{**}	C
5	HB-(M)-1×HB-43	177.00^{**}	6.83^{**}	-2.67	-85.33^{**}	29.83^{**}	D
6	HB-(M)-1 × EC-117705	164.33^{**}	12.17^{**}	1.78	-51.56^{**}	39.61^{**}	C
7	Vikrant × HB-43	158.33^{**}	8.67^{**}	-17.78^{**}	-17.78^{**}	28.89^{**}	D
8	Vikrant × EC-117705	177.67^{**}	13.50^{**}	32.67^{**}	-184.00^{**}	79.17^{**}	C
9	Vikrant × EC-621829	168.00^{**}	9.17^{**}	-10.22^{**}	-40.89^{**}	27.28^{**}	D
	Plant height						
1	HB-85 × HB-43	85.20^{**}	9.33^{**}	-26.40^{**}	191.46^{**}	-31.95^{**}	C
2	HB-85 × EC-117705	86.39^{**}	12.53^{**}	-21.74^{**}	168.36^{**}	-18.22^{**}	C
3	HB-86 × HB-8	88.29^{**}	-8.60^{**}	1.89	140.99^{**}	-46.65^{**}	D
4	HB-86 × EC-117705	87.96^{**}	-1.79^{*}	-12.81^{**}	131.27^{**}	-43.26^{**}	C
5	HB-(M)-1×HB-43	94.49^{**}	8.71^{**}	13.26^{**}	52.10^{**}	15.01^{**}	C
6	HB-(M)-1 × EC-117705	84.97^{**}	8.72^{**}	-13.69^{**}	226.48^{**}	-39.40^{**}	C
7	Vikrant × HB-43	91.60^{**}	5.80^{**}	-4.42^{*}	140.71^{**}	-24.02^{**}	C
8	Vikrant × EC-117705	84.72^{**}	9.02^{**}	-20.55^{**}	319.01^{**}	-69.67^{**}	C
9	Vikrant × EC-621829	99.29^{**}	21.36^{**}	23.79^{**}	35.74^{**}	22.44^{**}	C

	Branches per plant						
1	HB-85 × HB-43	3.95**	-015**	-1.24**	16.59**	-4.08**	C
2	HB-85 × EC-117705	3.73**	0.46**	-2.09**	11.41**	-2.34**	C
3	HB-86 × HB-8	5.48**	-0.52**	5.26**	1.14	1.09**	C
4	HB-86 × EC-117705	3.90**	0.43**	-0.36	15.22**	-2.97**	C
5	HB-(M)-1×HB-43	3.68**	-0.52**	1.15**	8.87**	-2.18**	D
6	HB-(M)-1 × EC-117705	4.33**	-0.44**	1.67**	7.85**	-2.45**	D
7	Vikrant × HB-43	4.23**	-0.99**	2.74**	-0.51	-0.84**	D
8	Vikrant × EC-117705	3.51**	-0.48**	-2.06**	16.73**	-5.87**	C
9	Vikrant × EC-621829	4.55**	-0.06	-0.58**	13.77**	-4.81**	C

Table 3 b. Gene effects estimated by five parameter model (Hayman, 1958).

	Cross	m	d	h	i	l	Epistasis
	Cluster per plant						
1	HB-85 × HB-43	14.31**	-2.48**	1.28**	73.59**	-17.45**	D
2	HB-85 × EC-117705	12.52**	-0.67**	-11.07**	75.88**	-20.53**	C
3	HB-86 × HB-8	16.77**	-1.73**	-3.72**	66.24**	-20.10**	C
4	HB-86 × EC-117705	17.53**	0.08	-0.5	56.52**	-14.79**	C
5	HB-(M)-1×HB-43	16.40**	-2.43**	-0.29	46.58**	-14.06**	C
6	HB-(M)-1 × EC-117705	17.53**	-2.34**	3.80**	48.69**	-15.01**	D
7	Vikrant × HB-43	20.08**	-4.85**	8.38**	3.58*	-8.59**	D
8	Vikrant × EC-117705	10.80**	-2.59**	-10.37**	91.09**	-27.68**	C
9	Vikrant × EC-621829	16.88**	1.16*	-4.71**	62.13**	-18.48**	C
	Pod length						
1	HB-85 × HB-43	3.32**	0.08**	-2.68**	14.81**	-3.18**	C
2	HB-85 × EC-117705	3.92**	0.10**	-2.27**	11.89**	-2.61**	C
3	HB-86 × HB-8	5.29**	0.32**	-0.30**	4.74**	-0.26*	C
4	HB-86 × EC-117705	4.61**	0.33**	-2.13**	9.30**	-1.81**	C
5	HB-(M)-1×HB-43	4.98**	0.50**	-1.97**	8.88**	-1.66**	C
6	HB-(M)-1 × EC-117705	5.44**	0.51**	-0.13**	5.65**	-0.29**	C
7	Vikrant × HB-43	5.39**	0.10*	0.97**	2.08**	-0.06	D
8	Vikrant × EC-117705	4.18**	0.03	-0.98**	6.62**	-1.22**	C
9	Vikrant × EC-621829	5.23**	-0.76**	-1.28**	6.72**	-3.17**	C
	Pods per plant						
1	HB-85 × HB-43	34.61**	-0.62	-22.40**	238.88**	-54.87**	C
2	HB-85 × EC-117705	31.35**	2.01	-16.05**	178.05**	-37.94**	C
3	HB-86 × HB-8	39.59**	-5.41**	-22.74**	146.25**	-56.34**	C
4	HB-86 × EC-117705	40.79**	-0.42	-8.77**	142.68**	-44.10**	C
5	HB-(M)-1×HB-43	34.82**	-6.36**	-4.05*	144.96**	-42.85**	C
6	HB-(M)-1 × EC-117705	39.42**	-5.66**	1.8	174.04**	-54.44**	D
7	Vikrant × HB-43	45.04**	-11.52**	17.08**	17.48**	-23.09**	D
8	Vikrant × EC-117705	29.53**	-5.36**	-21.39**	182.80**	-60.09**	C
9	Vikrant × EC-621829	38.7	2.39*	-9.59**	127.47**	-38.49**	C
	Seed per pod						
1	HB-85 × HB-43	2.92**	0.47	-0.68**	3.64**	-1.21**	C
2	HB-85 × EC-117705	2.91**	0.03	-0.91**	4.40**	-1.34**	C
3	HB-86 × HB-8	3.15**	0.35**	0.64**	1.17**	0.95**	C
4	HB-86 × EC-117705	3.51**	0.48**	-0.06	2.02**	0.40**	D
5	HB-(M)-1×HB-43	3.50**	0.50**	-1.74**	6.11**	-1.34**	C
6	HB-(M)-1 × EC-117705	3.76**	0.42**	0.48**	0.34*	0.72**	C
7	Vikrant × HB-43	3.37**	0.01	0.68**	-0.39**	0.13**	C
8	Vikrant × EC-117705	2.91**	0.03	-0.37**	4.12**	-1.11**	C
9	Vikrant × EC-621829	3.20**	0.03	-0.12**	2.19**	-0.69**	C
	100 seed weight						
1	HB-85 × HB-43	26.71**	0.84**	-4.24**	25.56**	-4.47**	C

2	HB-85 × EC-117705	27.58**	-0.29*	-4.40**	16.69**	-4.04**	C
3	HB-86 × HB-8	25.04**	-0.49**	-3.15**	24.79**	-7.43**	D
4	HB-86 × EC-117705	26.46**	-1.72**	-4.73**	24.91**	-9.81**	C
5	HB-(M)-1×HB-43	28.65**	1.11**	-5.58**	8.31**	-1.88**	C
6	HB-(M)-1 × EC-117705	33.33**	-0.21	8.71**	-21.48**	6.21**	C
7	Vikrant × HB-43	23.22**	-0.06	-7.88**	43.80**	-10.39**	C
8	Vikrant × EC-117705	26.53**	-1.28**	-5.16**	34.35**	-10.86**	C
9	Vikrant × EC-621829	27.39**	-4.30**	-5.35**	24.10**	-13.04**	C
	Yield per plant						
1	HB-85 × HB-43	30.95**	-0.25	-27.32**	308.17**	-75.47**	C
2	HB-85 × EC-117705	29.55**	0.67	-24.61**	238.26**	-57.51**	C
3	HB-86 × HB-8	34.38**	-2.25	-12.59**	183.46**	-50.98**	C
4	HB-86 × EC-117705	40.56**	2.26	-18.72**	235.16**	-63.50**	C
5	HB-(M)-1×HB-43	38.80**	1.19	-30.25**	242.58**	-64.68**	C
6	HB-(M)-1 × EC-117705	51.50**	-1.39	21.32**	213.29**	-52.67**	D
7	Vikrant × HB-43	39.74**	-10.18**	4.08**	111.50**	-47.68**	D
8	Vikrant × EC-117705	26.94**	-6.74**	-9.67**	250.29**	-71.97**	C
9	Vikrant × EC-621829	35.86**	-1.93*	-12.47**	187.45**	-60.24**	C

* Significant at 5% ** Significant at 1%

Table 4 a. Gene effects estimated by joint scaling test (Cavalli, 1952).

	Cross	m	d	h	i	l	Epistasis
	Days to 50%flowering						
1	HB-85 × HB-43	49.67**	-8.17**	89.67**	13.06**	-86.00**	D
2	HB-85 × EC-117705	64.40**	-6.01**	-35.93**	0.08	23.86**	D
3	HB-86 × HB-8	60.16**	-2.50**	24.41**	0.08	-30.56**	D
4	HB-86 × EC-117705	55.67**	-4.90**	40.67**	10.83**	-44.00**	D
5	HB-(M)-1×HB-43	68.62**	2.05*	29.93**	0.23	-39.56**	D
6	HB-(M)-1 × EC-117705	67.91**	2.36**	-5.41**	0	0	-
7	Vikrant × HB-43	64.00**	11.60**	-19.08**	1.72	6.00**	D
8	Vikrant × EC-117705	59.67**	4.78**	41.67**	4.67**	-43.33**	D
9	Vikrant × EC-621829	68.00**	-4.77**	35.94**	0.17	-42.27**	D
	Days to maturity						
1	HB-85 × HB-43	152.33**	3.78**	84.67**	10.98**	-81.33**	D
2	HB-85 × EC-117705	167.67**	-6.81**	-72.67**	-8.73**	52.00**	D
3	HB-86 × HB-8	156.00**	-1.24	50.33**	4.75**	-52.67**	D
4	HB-86 × EC-117705	152.67**	2.19**	72.00**	7.48**	-74.67**	D
5	HB-(M)-1×HB-43	172.73**	6.43**	34.52**	0.99	-52.92**	D
6	HB-(M)-1 × EC-117705	163.48**	12.17**	0	2.36**	-10.35**	-
7	Vikrant × HB-43	163.77**	8.67**	8.50**	10.56**	-19.94**	D
8	Vikrant × EC-117705	138.33**	5.67**	147.67**	38.35**	-138.00**	D
9	Vikrant × EC-621829	170.10**	7.59	5.42**	0.05	-22.86**	D
	Plant height						
1	HB-85 × HB-43	122.34**	5.46**	-146.06**	-35.04**	143.59**	D
2	HB-85 × EC-117705	118.30**	15.04**	-126.96**	-23.74**	126.27**	D
3	HB-86 × HB-8	96.60**	-11.37**	-45.70**	0.89	73.57**	D
4	HB-86 × EC-117705	110.78**	9.16**	-94.85**	-23.95**	98.45**	D
5	HB-(M)-1×HB-43	97.68**	7.92**	-29.90**	-12.78**	46.37**	D
6	HB-(M)-1 × EC-117705	120.12**	15.30**	-155.24**	-29.04**	169.86**	D
7	Vikrant × HB-43	111.40**	2.30**	-96.34**	-12.69**	105.53**	D
8	Vikrant × EC-117705	134.88**	25.11**	-219.94**	-41.43**	239.26**	D
9	Vikrant × EC-621829	92.30**	21.36**	0.08	-16.25**	27.86**	C

	Branches per plant						
1	HB-85 × HB-43	6.64^{**}	0.16	-11.61^{**}	-1.58	12.44^{**}	D
2	HB-85 × EC-117705	6.21^{**}	2.43^{**}	-9.23^{**}	-1.58	8.56^{**}	D
3	HB-86 × HB-8	2.75^{**}	-0.52	5.54^{**}	2.50^{**}	0.93	D
4	HB-86 × EC-117705	5.98^{**}	1.16	-9.87^{**}	-2.04^{*}	11.41^{**}	D
5	HB-(M)-1×HB-43	4.19^{**}	-0.52	-4.31^{**}	-1.88	6.59^{**}	D
6	HB-(M)-1 × EC-117705	4.47^{**}	2.18^{*}	-3.24^{**}	-0.56	5.89^{**}	D
7	Vikrant × HB-43	2.84^{**}	-0.99	0.47	1.04	0.45	C
8	Vikrant × EC-117705	6.63^{**}	0.38	-12.51^{**}	-2.79^{**}	12.55^{**}	D
9	Vikrant × EC-621829	6.57^{**}	0.42	-9.19^{**}	-2.96^{**}	10.33^{**}	D
	Cluster per plant						
1	HB-85 × HB-43	22.87^{**}	-3.18^{**}	-44.71^{**}	-1.24	55.19^{**}	D
2	HB-85 × EC-117705	27.54^{**}	1.45	-58.5	-10.21^{**}	56.91^{**}	D
3	HB-86 × HB-8	26.91^{**}	3.18^{**}	-45.12^{**}	-18.48^{**}	49.68^{**}	D
4	HB-86 × EC-117705	24.84^{**}	0.08	-35.82^{**}	-7.94^{**}	42.39^{**}	D
5	HB-(M)-1×HB-43	19.35^{**}	-2.54^{**}	-10.58^{**}	-4.77^{**}	19.13^{**}	D
6	HB-(M)-1 × EC-117705	21.72^{**}	-2.41^{**}	-26.63^{**}	-2.44^{**}	36.52^{**}	D
7	Vikrant × HB-43	16.10^{**}	-4.85^{**}	-4.36^{**}	1.81	0.81	D
8	Vikrant × EC-117705	27.37^{**}	-6.28^{**}	-67.31^{**}	-9.89^{**}	68.32^{**}	D
9	Vikrant × EC-621829	27.00^{**}	0.09	-43.54^{**}	-13.06^{**}	46.60^{**}	D

Table 4 b. Gene effects estimated by joint scaling test (Cavalli, 1952).

	Cross	m	d	h	i	l	Epistasis
	Pod length						
1	HB-85 × HB-43	6.51^{**}	3.90^{**}	-11.94^{**}	-1.53	11.11^{**}	D
2	HB-85 × EC-117705	6.54^{**}	5.46^{**}	-9.70^{**}	-1.28	8.92^{**}	D
3	HB-86 × HB-8	5.75^{**}	0.34	-2.32^{**}	-7.40^{**}	2.90^{**}	D
4	HB-86 × EC-117705	6.84^{**}	-0.99	-7.94^{**}	-1.64^{**}	6.97^{**}	D
5	HB-(M)-1×HB-43	7.07^{**}	0.14	-7.52^{**}	-1.29	6.66^{**}	D
6	HB-(M)-1 × EC-117705	5.88^{**}	0.26	-2.32^{**}	0.09	3.24^{**}	D
7	Vikrant × HB-43	5.16^{**}	0.09	-0.78	0.15	1.56^{**}	D
8	Vikrant × EC-117705	5.50^{**}	-0.33	-5.12^{**}	-0.46	4.97^{**}	D
9	Vikrant × EC-621829	6.14^{**}	-0.85	-3.26^{**}	1.19	3.39^{**}	D
	Pods per plant						
1	HB-85 × HB-43	75.67^{**}	2.13^{*}	-171.70^{**}	-24.16^{**}	179.16^{**}	D
2	HB-85 × EC-117705	61.63^{**}	24.61^{**}	-127.33^{**}	-19.37^{**}	133.54^{**}	D
3	HB-86 × HB-8	69.24^{**}	71.89^{**}	-114.15^{**}	-25.14^{**}	109.69^{**}	D
4	HB-86 × EC-117705	63.01^{**}	-24.78^{**}	-97.94^{**}	-25.12^{**}	107.01^{**}	D
5	HB-(M)-1×HB-43	43.64^{**}	-6.45^{**}	-50.27^{**}	0	75.67^{**}	D
6	HB-(M)-1 × EC-117705	60.27^{**}	2.14^{*}	-106.97^{**}	-16.46^{**}	130.53^{**}	D
7	Vikrant × HB-43	40.43^{**}	-11.58^{**}	-9.16^{**}	0.33	17.80^{**}	D
8	Vikrant × EC-117705	63.08^{**}	-11.16^{**}	-135.64^{**}	-27.11^{**}	137.10^{**}	D
9	Vikrant × EC-621829	59.42^{**}	18.77^{**}	-89.25^{**}	-27.95^{**}	95.60^{**}	D
	Seed per pod						
1	HB-85 × HB-43	3.72^{**}	0.16	-2.95^{**}	-0.76	2.73^{**}	D
2	HB-85 × EC-117705	3.91^{**}	0.48	-3.66^{**}	-0.86	3.30^{**}	D
3	HB-86 × HB-8	2.96^{**}	0.35	0.11	0.41	0.8	C
4	HB-86 × EC-117705	3.51^{**}	0.47	-0.28	0.88	0.75	D
5	HB-(M)-1×HB-43	5.13^{**}	0.58	-5.56^{**}	-1.69	4.58^{**}	D
6	HB-(M)-1 × EC-117705	3.51^{**}	0.43	0.56	0.61	0.88	D
7	Vikrant × HB-43	2.98^{**}	0.49	0.13	0.07	-0.29	D
8	Vikrant × EC-117705	3.61^{**}	2.88^{**}	-2.95^{**}	-0.65	3.09^{**}	D
9	Vikrant × EC-621829	3.53^{**}	1.18	-1.49	-0.49	1.64	D
	100 seed weight						
1	HB-85 × HB-43	32.02^{**}	-4.82^{**}	-20.21^{**}	-3.65^{**}	19.17^{**}	D

2	HB-85 × EC-117705	31.87**	0.71	-14.83**	-1.25	12.52**	D
3	HB-86 × HB-8	29.72**	4.28**	-18.64**	-2.88**	18.59**	D
4	HB-86 × EC-117705	31.94**	0.78	-20.30**	-4.12**	18.68**	D
5	HB-(M)-1×HB-43	32.48**	0.78	-10.77**	-3.13**	6.23**	D
6	HB-(M)-1 × EC-117705	26.29**	1.57	22.14**	3.75**	-16.11**	D
7	Vikrant × HB-43	32.63**	6.94**	31.56**	-4.78**	32.85**	D
8	Vikrant × EC-117705	33.41**	-8.27	-26.63**	-3.77**	25.76**	D
9	Vikrant × EC-621829	32.08**	-4.48**	-16.91**	0.16	15.57**	D
	Yield per plant						
1	HB-85 × HB-43	83.13**	2.87**	-219.92**	-36.43**	231.13**	D
2	HB-85 × EC-117705	71.64**	3.61**	-173.52**	-28.92**	178.69**	D
3	HB-86 × HB-8	63.60**	-9.75**	-127.25**	-22.25**	137.59**	D
4	HB-86 × EC-117705	79.32**	-8.68**	-165.69**	-40.00**	176.37**	D
5	HB-(M)-1×HB-43	84.24**	16.18**	-181.86**	-36.40**	181.93**	D
6	HB-(M)-1 × EC-117705	67.50**	6.83**	-111.98**	-22.15**	159.97**	D
7	Vikrant × HB-43	51.64**	-5.17	-48.73**	-5.47**	83.63**	D
8	Vikrant × EC-117705	63.06**	9.48	-166.10**	-25.66**	187.72**	D
9	Vikrant × EC-621829	65.53**	-6.16**	-129.63**	-32.75**	140.59**	D

* Significant at 5% ** Significant at 1%

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