Genetics of Quantitative Traits in Dolichos Bean (*Lablab purpureus* L. Sweet) Var. Lignosus

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Abstract

Most reported attempts to unravel genetics of quantitative traits (QTs) are based on either first or second degree statistics, but, rarely both. The use of both first and second degree statistics provide the most comprehensive mode of action of genes controlling QTs in crop plants. Genetics of fresh pod yield and its component traits was unravelled using the combination of first and second degree statistics in dolichos bean. The results based solely on first and second degree statistics were contradictory. While, first degree statistics suggested the predominance of genes with dominance effects, second degree statistics indicated the predominance of additive gene effects in controlling the inheritance of most QTs investigated. On the other hand, the combination of first and second degree statistics revealed the importance of both additive and dominance genetic effects in the inheritance of plant height and raceme length. High magnitude of the estimates of additive gene effects [d] and additive genetic variance (σ^2_A) coupled with low magnitude / non-significant dominance gene effects [h] and non-significant dominance genetic variance (σ^2_D) suggested high frequency of increasing effect genes controlling the inheritance of dry pods plant^{-1}, dry pod weight plant^{-1} and dry seed weight plant^{-1}. Bi-parental mating in F_2 generations before selection is suggested to reduce dominance genetic effects to increase the effectiveness of selection for plant height and raceme length. Simple selection on the basis of F_3 family means is expected to result in rapid genetic gain in dry pods plant^{-1}, dry pod weight plant^{-1} and dry seed weight plant^{-1}.

Dolichos bean (*Lablab purpureus* L. Sweet) is one of the most ancient legume crops known for its food (Ayyangar and Nambiar, 1935; Vishwanath *et al.,* 1971) and fodder (Magoon *et al.,* 1974) values. Dolichos bean var. Lignosus is predominantly produced for immature beans for use as a vegetable in southern parts of Karnataka state in India (Vishwanath *et al.,* 1971; Shivashankar and Kulkarni, 1989). It is predominantly a self-pollinated crop (Ayyangar and Nambiar, 1935) with 2n=2x=22 chromosomes (She and Jiang, 2015) and a genome size of 367 Mbp (Iwata *et al.,* 2013). Pedigree selection is the most commonly used method of handling segregating generations derived from crosses involving deliberately selected parents to develop high yielding pure-line varieties in dolichos bean. Effectiveness of breeding pure-line varieties hinges on precise knowledge on relative magnitudes of genetic variation and contribution of non-genetic sources. To elicit such genetic information, it is necessary to conceive the genetic model appropriate to the working genetic material that is intended for use in developing pure-line varieties.

Genetics of productivity *per se* traits could be unraveled at first and second degree statistics levels. Developing and testing the digenic epistasis-independent (additive-dominance model) and epistasis-inclusive models are the popular method of unraveling genetics of productivity *per se* traits at first degree statistics level (popularly known as generations mean analysis). Translating covariance of full-sib and half–sibs produced by diallel (Griffing, 1956) and line × tester mating designs (Kempthorne, 1957) into components of genotype variance and / or biometrical genetic analysis of progenies derived from standard triple test cross (TTC) (Kearsey and Jinks, 1968) and simplified TTC designs (Jinks *et al.,* 1969) are the most commonly used approaches to unravel the genetics of productivity *per se* traits at second degree statistics level. The reported literature indicates the use of either first degree or second degree statistics-based approaches and rarely both for genetic analysis of quantitative traits in crop plants. However, analysis of first and second degree statistics are not mutually exclusive alternatives, but, are genetically complementary to each other

(Mather and Jinks, 1982; Kearsey and Pooni, 1996). Joint application of both the approaches provides complementary and comprehensive information about genetic control of quantitative traits (Kearsey and Pooni, 1996).

However, such studies have not yet been attempted in dolichos bean. Under these premises, the present study was carried out with an objective to unravel, interpret and discuss dolichos bean breeding implications of genetic parameters estimated based on first and second degree statistics.

MATERIAL AND METHODS

Basic genetic material and development of experimental material :   The basic genetic material for the study consisted of three pairs of genotypes (1) P_1 (HA-10-8) and P_2 (RIL 3-180); (2) P_1 (HA-11-3) and P_2 (RIL 3-180); and (3) P_1 (FPB 21) and P_2 (RIL 3-180) contrasting for pod yield and its component traits (Keerthi *et al.,* 2016) (Table I). These were crossed to obtain three F_1s [(HA-10-8 × RIL 3-180), (HA-11-3 × RIL 3-180) and (FPB 21 × RIL 3-180)] during 2013 rainy season. The plants of the three F_1's were grown and selfed during 2013 post-rainy season. F_2 population derived from the three F_1's along with P_1, P_2 and F_1's were grown in 2014 rainy season at the experimental plot of the Department of Genetics and Plant Breeding (GPB), University of Agricultural Sciences (UAS), Bengaluru, India. The experimental plot is located at an altitude of 930 m above mean sea level at 12^0 58' North and $77^0$35' East latitude and longitude, respectively. A total of 160, 155 and 180 F_2

TABLE I

Pedigree of the parents of the three crosses used as experimental material in dolichos bean

Parent	Pedigree
HA-10-8	HA 4 × GL 153
HA-11-3	HA 4 × GL 127
FPB 21	Unknown
RIL 3-180	HA 4 × CPI 31113

plants derived from HA-10-8 × RIL 3-180; HA-11-3 × RIL 3-180; and FPB 21 × RIL 3-180 crosses, respectively could be maintained. The selfed seeds from the parents and 10 F_1's (to raise F_2 plants subsequently) and 30 random F_2 plants (to raise F_3 families subsequently) derived from the three crosses were collected, dried and stored in -20°C. A part of the seeds collected from F_2 plants derived from the three crosses were planted in plant-to-row progenies (which constituted F_3 families) in 2014 post-rainy season. Two random plants from each of the 20 randomly selected F_3 families derived from the three crosses were selfed, seeds were collected, dried and stored in -20°C for subsequently raising F_4 families. Due to poor germination of F_2 seeds derived from HA-11-3 × RIL 3-180 cross, F_3 and hence, F_4 families from this cross could not be raised. The five basic generations [P_1, P_2, F_1, F_2 and F_3 (30 families)] derived from three crosses (HA-10-8 × RIL 3-180; HA-11-3 × RIL 3-180; and FPB 21 × RIL 3-180); and F_4 generation (consisting of 2 × 20 = 40 F_4 families) derived from two crosses (HA-10-8 × RIL 3-180 and FPB 21 × RIL 3-180) constituted the experimental material.

Evaluation of experimental material :   The non-segregating generations P_1, P_2 and F_1's of the three crosses were evaluated in a randomized complete block design (RCBD) with two replications in experimental plot of Department of GPB, Bengaluru during 2015 rainy season. The seeds of P_1, P_2 and F_1's were sown in a single row of 3 m length. Ten days after sowing, the seedlings were thinned by maintaining intra-row spacing of 0.20 m within a row in each replication. The F_2 plants and 30 F_3 families each derived from the three crosses (HA-10-8 × RIL 3-180, HA-11-3 × RIL 3-180 and FPB 21 × RIL 3-180) and F_4 families each derived from two crosses (HA-10-8 × RIL 3-180 and FPB 21 × RIL 3-180) were evaluated in two separate contiguous blocks. The seeds of the F_2 plants were sown in 20 rows. Ten days after sowing, seedlings were thinned maintaining 10 plants in each row with intra-row spacing of 0.20 m and 0.45 m between rows. At the time of recording data, there were 187, 191 and 194 F_2 plants derived from HA-10-8 × RIL 3-180, HA-11-3 × RIL 3-180 and FPB 21 × RIL 3-180, respectively. Each of the 30 F_3 and 40 F_4 families were grown in a single row of 2 m length and 10 plants were maintained in each row with intra-row

spacing of 0.20 m and 0.45 m between rows. Data were recorded on five randomly selected plants in P_1, P_2 and F_1, all F_2 plants and 5 randomly selected plants from each F_3 and F_4 families on nine quantitative traits (Table II) based on dolichos bean descriptors (Byregowda *et al.*, 2015).

*Statistical analysis of data :*Mean of the data recorded on five plants in P_1, P_2, F_1 and data recorded on individual F_2, F_3 and F_4 plants were used for the following statistical analysis.

Estimation of first degree statistics-based gene effects : First degree statistics-based gene effects were estimated using the following perfect-fit solutions based on five parameter model (Hayman, 1958).

Statistical significance of gene effects was examined using 't' test (Mather and Jinks, 1982).

Estimation of second degree statistics-based genetics (components of genotypic variation)

Additive genetic variance (σ^2_A) : The σ^2_A was estimated using observed and expected mean sum of

squares (MSS) of analysis of variance (ANOVA) of F_3 families (Table III) (van Ooijen, 1989).

Dominance genetic variance (σ^2_D) : The σ^2_D was estimated using observed and expected MSS of ANOVA of F_4 families (Table IV) (Kearsey and Pooni, 1996). The analysis of quantitative trait data of F_4

$$[\hat{m}] = \bar{F}_2$$
$$[\hat{d}] = 1/2(\bar{P}_1 - \bar{P}_2)$$
$$[\hat{h}] = 2/3\bar{F}_1 - 2\bar{F}_2 - 8/3\bar{F}_3$$
$$[\hat{i}] = \bar{P}_1 - \bar{F}_2 + 1/2\bar{P}_1 - 1/2\bar{P}_2 + 1/2[d] - 1/4[l]$$
$$[\hat{l}] = 8/3\bar{F}_1 - 8\bar{F}_2 + 16/3\bar{F}_3$$

families results in 'nested' or hierarchical' ANOVA. Thus, total variability among F_4 progenies was partitioned into "between F_2 groups", "between F_3 groups within F_2 groups" and "between F_4 individuals within F_3 groups" (Table IV). The ANOVA of F_4 families provided another source of estimate of σ^2_A.

TABLE II

Procedure of recording data on nine quantitative traits in dolichos bean

Trits	Procedure of measurement
Plant height (cm)	The length of 5 randomly selected plants was measured from base of the plant to tip of the plant using standard metric scale and expressed in cm.
Primary branches plant^{-1}	Number of primary branches on 5 randomly selected plants were counted and averaged.
Racemes plant^{-1}	Number of racemes borne on 5 randomly selected plants were counted and averaged.
Raceme length (cm)	The length of 5 randomly selected racemes borne on 5 plants was measured using standard metric scale and averaged.
Dry pods raceme^{-1}	Number of sun-dried pods on 5 randomly selected racemes were counted and averaged.
Dry pods plant^{-1}	Number of sun-dried pods from 5 randomly chosen plants were counted and averaged.
Dry pods yield plant^{-1} (g)	Sun- dried pod yield of 5 randomly chosen plants were weighed in grams and averaged.
Dry seed yield plant^{-1} (g)	Sun- dried seeds shelled from sun-dried pods borne on 5 randomly selected plants are weighed in grams and averaged.
100-dry seed weight (g)	100 sun-dried seeds were weighed and expressed in grams.

<center>TABLE III</center>

Stricture of analysis of F_3 families in dolichos bean

Source	Degrees of freedom	Observed Mean sum of squares (MSS)	Expected MSS
Between families	f-1	MS_b	$s^2_w + ns^2_b$
Within families	f(n-1)	MS_w	s^2_w

Where, f= Number of F_3 families; n= Number of plants within a family

As "between F_3 families" mean square was significant, σ^2_A were estimated assuming absence of σ^2_D (dominance genetic variance) using following formulae (van Ooijen, 1989).

$\sigma^2_b = MS_b - MS_w/n =$ Between F_3 family variance

$\sigma^2_w = MS_w =$ Within F_3 family variance

$\sigma^2_A = \sigma^2_b$

$\sigma^2_e = \sigma^2_w - 1/2\,\sigma^2_A$

Where, $\sigma^2_e =$ variance due to non-genetic sources.

<center>TABLE IV</center>

Structure of analysis variance of F_4 families in dolichos bean

Source	Degrees of freedom	Observed Mean sum of squares (MSS)	Expected MSS
Between F_2 groups	n-1	MS_1	$s^2_3 + rs^2_2 + n'\,rs^2_1$
Between F_3 groups within F_2 groups	n(n'-1)	MS_2	$s^2_3 + rs^2_2$
Between F_4 individuals within F_3 groups	nn'(r-1)	MS_3	s^2_3
Total	nn'r-1		

Where n= Number of F_2 groups

n' = Number of F_3 groups within each F_2 group

r= Number of individuals in F_4

σ^2_A, σ^2_D and environmental variance (σ^2_e) were estimated by solving following equations in σ^2_1 and σ^2_2 and σ^2_3

$\sigma^2_1 = (MS_1 - MS_2)/n'r$; $\sigma^2_2 = (MS_2 - MS_3)/r$

$\sigma^2_1 = \frac{1}{2}\,\sigma^2_A + 1/64\,\sigma^2_D$; $\sigma^2_2 = \frac{1}{4}\sigma^2_A + 1/32\sigma^2_D$

$\sigma^2_3 = \frac{1}{2}\,\sigma^2_A + 1/16\,\sigma^2_D + \sigma^2_e$

Phenotypic variance (σ^2_p) was estimated as, $\sigma^2_p = \sigma^2_A + \sigma^2_D + \sigma^2_e$,

Where, $\sigma^2_e = \sigma^2_w - \frac{1}{2}\,\sigma^2_A$; $\sigma^2_w = MS_2$

Where, $\sigma^2_e =$ variance due to non genetic sources.

Interpretation of mode of action of genes based on the combinations of first and second degree statistics-based parameters

Based on the combinations of the magnitude and direction of the estimates of additive genetic effects [d] and additive genetic variance (σ^2_A) and dominance genetic effects (h) and dominance genetic variance (σ^2_D), the results are interpreted (Kearsey and Pooni, 1996) as indicated in Table V and Table VI, respectively.

<div align="center">RESULTS AND DISCUSSION</div>

First degree statistics-based genetics : Additive-dominance (A-D) model was inadequate to explain the expression of all the traits except plant height in HA 10-8 × RIL 3-180 and FPB 21 × RIL 3-180 and for primary branches plant[-1] in HA 10-8 × RIL 3-180 and HA 11-3 × RIL 3-180 as indicated by the significance of joint-scaling test (Table VII). Pathak *et al.* (2014) in mung bean detected non-adequacy of A-D model in the inheritance of most of the traits. Non-adequacy of A-D model in the present study could be attributed to non-inclusion of parameters specifying digenic epistasis and / or genotype × environment interaction. However, in the present study only parameters specifying digenic epistasis were included in the model and were estimated and interpreted (Mather and Jinks, 1982; Kearsey and Pooni, 1996).

<div align="center">TABLE V</div>

<div align="center">*Interpretation based on additive genetic effects (d) and additive genetic variance (σ^2_A) in dolichos bean*</div>

Additive genetic effects (d)	Additive genetic variance ($\acute{o}^2_A$)	Interpretation
Small and non-significant	Large and significant	Dispersion of increasing and decreasing alleles between parents hence mutual cancellation of effects of increasing and decreasing alleles
Large and significant	Large and significant	Prevalence of large additive gene effects
Large and significant	Small and non-significant	Effects of individual gene controlling trait are very small.

<div align="center">TABLE VI</div>

<div align="center">*Interpretation based on combination of dominance genetic effects (h) and dominance genetic variance ($\acute{o}^2_D$) in dolichos bean*</div>

Dominance genetic effects (h)	Dominance genetic variance ($\acute{o}^2_D$)	Interpretation
Significant postive	Significant	Directional dominance for increasing alleles
Significant negative	Significant	Directional dominance for decreasing alleles
Non-significant	Significant	Ambi-directionaldominance
Non-significant	Non-significant	No dominance
Significant, small	Non-significant	Low dominance

TABLE VII

Estimates of gene effects for dry pod yield and its contributing traits in three crosses in dolichos bean

Traits	Crosses	[m̂]	[d̂]	[ĥ]	χ² Statistic	Probability	Adequacy of additive Dominance (A+D) model
Plant height (cm)	HA 10-8×RIL 3-180	55.20**±1.50	-9.30**±2.18	13.21**±2.14	2.55	0.27	Adequate
	FPB 21× RIL 3-180	54.88**±1.42	-9.58**±1.52	14.07**±3.22	2.05	0.35	Adequate
	HA 11-3× RIL 3-180	50.73**±1.61	10.67**±2.17	19.66**±3.20	32.72	0.00	Not Adequate
Primary branches plant⁻¹	HA 10-8× RIL 3-180	2.5*±0.09	0.14±0.15	0.60**±0.21	6.27	0.10	Adequate
	FPB 21× RIL 3-180	2.43 ± 0.17	0.66** ± 0.53	1.84** ± 0.19	62.94	0.00	Not Adequate
	HA 11-3× RIL 3-180	3.04**±0.15	0.61**±0.22	-0.29 ± 0.34	2.98	0.39	Adequate
Racemes plant⁻¹	HA 10-8× RIL 3-180	6.52* ± 0.43	-1.33* ± 0.53	5.89 **± 0.67	67.37	0.00	Not Adequate
	FPB 2 × RIL 3-180	6.41**±0.32	-0.26±0.53	1.40±0.66	23.12	0.00	Not Adequate
	HA 11-3× RIL 3-180	3.20**±0.43	-0.39±0.71	4.55**±0.89	38.93	0.00	Not Adequate
Raceme length (cm)	HA 10-8× RIL 3-180	8.12** ± 0.18	-0.30 ± 0.23	2.62** ± .477	17.58	0.00	Not Adequate
	FPB 21× RIL 3-180	9.98**±0.40	-4.44**±0.60	6.81**±0.84	50.911	0.00	Not Adequate
	HA 11-3× RIL 3-180	9.66**±0.27	-2.48**±0.52	4.29**±0.59	2.33	0.03	Not Adequate
Dry pods raceme⁻¹	HA 10-8× RIL 3-180	3.57**±0.16	-0.17±0.19	3.28**±0.33	19.59	0.00	Not Adequate
	FPB 21× RIL 3-180	6.55**±0.12	-3.21**±0.133	-0.82*±0.37	61.66	0.00	Not Adequate
	HA 11-3× RIL 3-180	3.80**±0.30	0.34±0.322	5.28**±0.58	26.34	0.00	Not Adequate
Dry pods plant⁻¹	HA 10-8× RIL 3-180	18.98**±1.85	-7.90**±2.18	25.73**±2.68	6.29	0.04	Not Adequate
	FPB 21× RIL 3-180	14.71**±1.59	-5.70**±1.89	28.62**±3.30	54.18	0.00	Not Adequate
	HA 11-3× RIL 3-180	16.56**±2.20	5.75±2.58	25.46**±4.21	26.24	0.00	Not Adequate
Dry pod weight plant⁻¹ (g)	HA 10-8× RIL 3-180	17.96** ± 1.87	-8.26** ± 1.94	23.77** ± 3.71	7.61	0.02	Not Adequate
	FPB 21× RIL 3-180	20.45** ± 1.55	-10.68** ± 1.63	19.64** ± 3.01	12.05	0.00	Not Adequate
	HA 11-3× RIL 3-180	16.9** ± 2.82	6.82** ± 2.46	24.33** ± 4.13	19.67	0.00	Not Adequate
Dry seed weight plant⁻¹ (g)	HA 10-8× RIL 3-180	13.87** ± 2.2	-6.34** ± 2.3	23.01** ± 4.09	6.07	0.04	Not Adequate
	FPB 21× RIL 3-180	15.42** ± 2.19	-7.88** ± 1.54	15.97** ± 2.69	13.225	0.00	Not Adequate
	HA 11-3× RIL 3-180	9.41** ± 5.29	2.08 ± 1.93	24.61** ± 3.23	38.71	0.00	Not Adequate
100 dry seed weight (g)	HA 10-8× RIL 3-180	16.99** ±0.131	-1.73* ±0.143	2.99** ± 0.36	51.385	0.00	Not Adequate
	FPB 21 × RIL 3-180	17.00** ± 0.15	-1.91** ± 0.16	2.53** ± 0.34	12.18	0.00	Not Adequate
	HA 11-3× RIL 3-180	17.20** ± 0.11	2.00** ± 0.11	2.80** ± 0.24	46.66	0.00	Not Adequate

* Significant @ P = 0.05;   ** Significant @ P = 0.01

The additive effect of genes reflects those effects which are expected to be manifested in a genotype to which the genes are being substituted for their alternate forms / alleles (Mather and Jinks, 1982; Kearsey and Pooni, 1996). Significant but low magnitude or non-significant additive genetic effects in the inheritance of most of the traits in three crosses (Table VIII) could be attributed to genes with either low magnitude of additive effects or those with different degrees of nullifying increasing and decreasing effects (Mather and Jinks, 1982; Kearsey and Pooni, 1996). First degree statistics is valuable for detection and estimation of additive, dominance and epistatic gene effects. However, it does have limitations. Distribution of increasing and decreasing effect genes between the parents causes serious bias to the estimates of additive and additive × additive gene effects. However, dominance [h] and dominance × dominance [l] gene effects are independent of the degree of gene distribution due to which the combined estimates of [h] and [l] could be considered to be the best representative of sign and magnitude of individual h's and l's, respectively. Hence, practically [h] and [l] are the only components which can safely be used to determine the type of epistasis may have influence on the observed *per se* performance of generations for quantitative traits (Mather and Jinks, 1982; Kearsey and Pooni, 1996).

Significant [h] and positive [l] suggested possible involvement of dominant decreasing effect genes displaying duplicate digenic epistasis. On the other hand, the traits such as primary branches plant^{-1} and dry pods plant^{-1} in FPB 21 × RIL 3-180 and raceme length in HA 10-8 × RIL 3-180 were controlled by dominant increasing effect genes displaying duplicate digenic epistasis as indicated by positive and negative estimates of [h] and [l], respectively. Thus, first degree statistics-based components of generation means suggest predominance of genes with dominance and dominance-based effects in the inheritance of most of the traits investigated. These results are in agreement with those reported by Rahman *et al.* (1999) and Desai *et al.* (2013). The estimates of [d], [h], [i] and [l] which are based on first degree statistics pose serious limitations on the interpretation due to internal cancellation of effects of genes in positive and negative

direction. Thus, the estimates of genetic components of generation means are most often under estimated. This is especially true as these estimates are based on data obtained from highly selected set of parents where gene dispersion may not be an unusual phenomenon (Kearsey and Pooni, 1996). However, the estimates of variances (second degree statistics) arising from additive, dominance and di-genic epistatic effects of genes are not affected by internal cancellation of gene effects in positive and negative direction (Mather and Jinks, 1982; Kearsey and Pooni, 1996).

Second degree statistics-based genetics : In the absence of backcross generations, it is not possible to estimate additive genetic variance (σ^2_A) and dominance genetic variance (σ^2_D). However, while analysis of variance of F_3 families provides unbiased estimates of σ^2_A that of F_4 families provide unbiased estimate of both σ^2_A and σ^2_D. Analysis of variance of F_3 families revealed highly significant mean squares attributable to 'between F_3 families' for all the quantitative traits except for raceme length and dry pods raceme^{-1} in HA 10-8 × RIL 3-180 and for dry pods raceme^{-1} in FPB 21 × RIL 3-180 (Tables IX A & IX B). The estimates of σ^2_A were high for most of the quantitative traits in FPB 21 × RIL 3-180 compared to those in HA 10-8 × RIL 3-180 and HA 11-3 × RIL 3-180 (Table X). Analysis of variance of F_4 families revealed highly significant mean squares attributable to 'between F_2 groups' for all the quantitative traits in HA 10-8 × RIL 3-180 and FPB 21 × RIL 3-180. Mean squares attributable to 'between F_3 groups within F_2 groups' was significant for plant height, raceme length and 100 dry seed weight HA 10-8 × RIL 3-180 and FPB 21 × RIL 3-180 (Tables XI A and XII B). The estimates of σ^2_A were higher than σ^2_D for all the quantitative traits in both the crosses (Table XII). Das *et al.* (2014), Keerthi *et al.* (2015) and Chandrakant *et al.* (2015) also documented the predominance of additive genetic variance in controlling most of the quantitative traits in dolichos bean. Thus, contrary to first degree statistics (which revealed predominance of dominance genetic effects), second degree statistics revealed predominance of genes with additive effects. Thus, inferences solely based on either first or second degree statistics-based mode of action of genes controlling target traits are most often mislead. The

TABLE VIII

Estimates of digenic epistatic effects of traits for which Additive – Dominance model is inadequate in dolichos bean

Traits	Crosses	[m̂]	[d̂]	[ĥ]	[î]	[ĵ]	Type digenic epistasis
Plant height (cm)	HA 11-3 × RIL 3-180	52.54** ±4.02	12.96** ± 2.22	-19.38 ± 17.23	5.51 ±4.59	44.46** ± 14.37	DEBDDEG
Primary branches plant[-1]	FPB 21 × RIL 3-180	-2.07** ± 0.13	-0.2 ± 0.15	15.51** ± 0.8	4.67** ± 0.207	-10.63** ± 0.76	DEBDIEG
Racemes plant[-1]	HA 10-8 × RIL 3-180	7.11** ± 1.53	-2.24** ± 0.54	-7.28 ± 5.34	1.89 ± 1.62	14.06 **± 3.99	DEBDDEG
	FPB 21 × RIL 3-180	8.32** ± 0.69	0.20 ± 0.54	-5.21 ± 3.35	-3.92** ± 0.88	4.29 ± 2.88	DEBDDEG
	HA 11-3 × RIL 3-180	4.51** ± 0.75	2.70** ± 0.97	-6.11 ± 3.23	2.78** ± 1.22	11.40** ± 2.82	DEBDDEG
Raceme length (cm)	HA 10-8 × RIL 3-180	10.19** ± 0.56	-0.62** ± 0.23	9.04** ± 3.00	-4.41** ± 0.61	-12.41** ± 2.61	DEBDIEG
	FPB 21 × RIL 3-180	11.30** ± 0.80	-6.29** ± 0.69	-6.47 ± 3.61	1.75 ± 1.06	14.41** ± 3.12	DEBDDEG
	HA 11-3 × RIL 3-180	16.83** ± 1.28	5.89** ± 0.99	-8.66 ± 5.00	-4.18** ± 1.62	11.29** ± 3.96	DEBDDEG
Dry pods raceme[-1]	HA 10-8 × RIL 3-180	4.09** ± 0.33	-0.76** ± 0.28	-0.59 ± 1.41	0.14 ± 0.43	3.94** ± 1.20	DEBDDEG
	FPB 21 × RIL 3-180	6.42 ** ± 0.57	-3.36** ± 0.13	-6.81** ± 2.21	0.42 ± 0.59	8.95** ± 1.89	DEBDDEG
	HA 11-3 × RIL 3-180	6.28** ± 0.68	0.64 ± 0.46	-6.34** ± 2.54	-2.16** ± 0.82	10.26** ± 2.07	DEBDDEG
Dry pods plant[-1]	HA 10-8 × RIL 3-180	24.92** ± 5.01	-10.00** ± 2.87	-4.91 ± 17.88	-2.42 ± 5.78	25.99 ± 13.52	DEBDDEG
	FPB 21 × RIL 3-180	-6.011 ± 3.97	-13.60** ± 2.23	100.62**± 18.78	31.21** ± 4.55	-47.81**± 15.95	DEBDIEG
	HA 11-3 × RIL 3-180	25.06** ± 4.10	18.50** ± 4.59	-31.02 ± 16.94	5.03 ± 6.15	55.36** ± 14.29	DEBDDEG
Dry pod weight plant[-1] (g)	HA 10-8 × RIL 3-180	24.16** ± 4.68	-10.55** ± 2.64	-9.38 ± 16.66	-3.81 ± 5.33	32.18** ± 13.48	DEBDDEG
	FPB 21 × RIL 3-180	44.47** ± 7.60	-10.00** ± 1.76	-64.71** ± 24.77	-24.00** ± 80	62.90** ± 18.12	DEBDDEG
	HA 11-3 × RIL 3-180	26.36** ± 4.64	16.12** ± 4.26	-30.09 ± 17.72	0.15 ± 6.3	50.94** ± 14.40	DEBDDEG
Dry seed weight plant[-1] (g)	HA 10-8 × RIL 3-180	20.89** ± 4.92	-9.24** ± 3.52	-11.51 ± 17.71	-4.03 ± 6.05	31.38* ± 14.18	DEBDDEG
	FPB 21 × RIL 3-180	35.56** ± 6.63	-8.48** ± 1.77	-56.11**±21.27	-19.46**± 6.8	54.78** ± 15.34	DEBDDEG
	HA 11-3 × RIL 3-180	19.75** ± 3.34	14.86** ± 4.08	-31.82** ± 12.79	2.72 ± 5.27	52.26** ± 10.47	DEBDDEG
100 dry seed weight (g)	HA 10-8 × RIL 3-180	19.34** ± 0.42	-1.55** ± 0.14	-3.09 ± 1.73	-2.79** ± 0.44	2.45 ± 1.59	DEBDDEG
	FPB 21 × RIL 3-180	18.95 ± 0.62	-1.8 ± 0.166	-3.29 ± 2.27	-2.15 ± 0.65	3.63 ± 1.79	DEBDDEG
	HA 11-3 × RIL 3-180	20.20** ± 0.87	2.00** ± 0.11	-1.47 ± 3.16	-3.20** ± 0.87	0.77 ± 2.40	DEBDDEG

DEBDDEG-Duplicate epistasis between dominant decreasing effect genes

DEBDIEG- Duplicate epistasis between dominant increasing effect genes

TABLE IX A

Analysis of variance of F_3 families derived from three crosses for quantitative traits to dolichos bean

Source of variation	Degrees of freedom			Mean sum of squares											
				Plant height (cm)			Primary branches plant^{-1}			Recemes plant^{-1}			Recemes length plant^{-1}		
	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3
Between F_3 families	22	19	22	394.14**	1082.34**	361.93**	0.63*	3.12**	1.92**	62.45**	68.32**	12.89**	4.98	11.96*	40.11**
Within F_3 families	92	80	92	174.50	254.7	69.60	0.33	0.46	0.93	9.43	9.77	5.46	4.62	6.02	16.85

* Significant @ P = 0.05; ** Significant @ P = 0.01 C_1: HA 10-8 × RIL 3-180; C_2: FPB 21 × RIL 3-180; C_3: HA 11-3 × RIL 3-180

TABLE IX B

Analysis of variance of F_3 families derived from thre crosses for quantitative traits in dolichos bean

Source of variation	Degrees of freedom			Mean sum of squares														
				Dry pods raceme^{-1}			Dry pods plant^{-1}			Dry pod weight plant^{-1} (g)			Dry seed weight plant^{-1} (g)			100 dry seed weight (g)		
	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3
Between F_3 families	22	19	22	2.49	7.26	12.06**	1228.38**	1175.61**	390.21*	1204.19**	1387.57**	538.12*	634.69*	1066.51**	278.54*	4.31**	0.36**	26.67**
Within F_3 families	92	80	92	1.69	4.83	4.70	208.63	414.49	177.26	201.68	384.73	157.36	121.32	204.17	85.52	1.94	0.08	4.21

* Significant @ P = 0.05; ** Significant @ P = 0.01 C_1: HA 10-8 × RIL 3-180; C_2: FPB 21 × RIL 3-180; C_3: HA 11-3 × RIL 3-180

TABLE X

Estimates of additive genetic variance($\acute{o}^2_A$) for quantitative traits in F_3 populations derived from three crosses in dolichos bean

Traits	Estimates of $\acute{o}^2_A$		
	HA 10-8 × RIL 3-180	FPB 21 × RIL 3-180	HA 11-3 × RIL 3-180
Plant height (cm)	9.55**	41.38**	12.71**
Primary branches plant^{-1}	0.01**	0.13**	0.04**
Racemes plant^{-1}	2.30**	2.92**	0.32**
Raceme length (cm)	0.02	0.29*	1.01**
Dry pods raceme-1	0.03	0.12	0.32**
Dry pods plant^{-1}	44.34**	38.05**	9.26**
Dry pod weight plant^{-1} (g)	43.58**	50.14**	16.55**
Dry seed weight plant^{-1} (g)	22.32**	43.11**	8.39**
100 dry seed weight (g)	0.10**	0.01**	0.97**

* Significant @ P = 0.05;   ** Significant @ P = 0.01

combination of components of means and of variances provides complementary and more comprehensive information on the true nature of genetic control of quantitative traits (Kearsey and Pooni, 1996).

Interpretation of combination of first - and second degree statistic-based genetic parameters: Non-significant and / or significant but low magnitude of additive genetic effect [d] coupled with large σ^2_A for plant height in FPB 21 × RIL 3-180 cross indicated dispersion of increasing and decreasing effects genes between parents. Dispersion of increasing and decreasing effects genes reduce the trait means of the genotypes while association increases them. The probability of genes being in dispersion phase could be minimized by random mating in F_2 genotypes before selecting desired pure-lines (Roy, 2000). Hanson (1959) showed that with F_2 inter-mating, the risk of losing desired alleles is less than with selfing. High magnitude of the estimates of both [d] and (σ^2_A) suggests high frequency of increasing effect genes controlling dry pods plant^{-1}, dry pod weight plant^{-1} and dry seed weight plant^{-1}. On the other hand, high magnitude of [d] and low magnitude of (σ^2_A) indicated small effect additive

genes controlling raceme length in all the three crosses (Table XIII). Hence, inferences based on the magnitudes of only first degree statistics-based additive gene effects are not advisable, because the distribution of positive and negative gene effects in the parents may result in different degrees of cancellation of effects in the expression of the traits means of generations (Mather and Jinks, 1982; Kearsey and Pooni, 1996). For the same reason, the magnitudes of additive gene effects do not necessarily reflect those of σ^2_A. High magnitude of the estimates of σ^2_A indicate long-term genetic gains as they could be exploited through the constellation of desired genes controlling dry pods plant^{-1}, dry pod weight plant^{-1} and dry seed weight plant^{-1} in pure-lines. This is because σ^2_A is fixable by selection and hence it is possible to predict response to selection.

Dominance genetic effect [h] and dominance genetic variance (σ^2_D) : Significant positive [h] and significant $\acute{o}^2_D$ indicated the role of increasing effect genes with directional dominance in controlling the inheritance of plant height in both the crosses (Table XIII). Significant negative estimate of [h] and

TABLE XIA

Analysis of variance of F₄ families derived from two crosses for quantitative traits in dolichos bean

| Source of variation | Degrees of freedom | | Mean sum of squares | | | | | | | |
| | | | Plant height (cm) | | Primary branches plant⁻¹ | | Recemes plant⁻¹ | | Recemes length plant⁻¹ | |
Crosses	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2
Between F_2 groups	19.00	21.00	882.98**	612.15**	0.76*	0.92**	37.89	32.59**	18.94**	18.19**
Between F_3 groups within F_2 groups	20.00	22.00	339.12*	238.95**	0.57	0.55	32.25	20.82*	8.46**	11.04**
Between F_4 individuals within F_3 groups	160.00	176.00	194.69	102.57	0.40	0.35	29.56	11.65	4.16	4.79

* Significant @ P = 0.05;   ** Significant @ P = 0.01 C_1: HA 10-8 × RIL 3-180; C_2: FPB 21 × RIL 3-180

TABLE XIB

Analysis of variance of F₄ families derived from two crosses for quantitative traits in dolichos bean

| Source of variation | Degrees of freedom | | Mean sum of squares | | | | | | | | | |
| | | | Dry pods raceme⁻¹ | | Dry pods plant⁻¹ | | Dry pod weight plant⁻¹ (g) | | Dry seed weight plant⁻¹ (g) | | 100 dry seed weight (g) | |
Crosses Crosses	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2
Between F_2 groups	19	21	2.79*	4.13**	1115.04**	565.78**	1215.48**	621.07**	582.28**	436.77**	8.73**	12.79**
Between F_3 groups within F_2 groups	20	22	1.94	1.83	575.01	310.48	672.96	294.36	338.85	212.71	4.08*	3.19*
Between F_4 individuals within F_3 groups	160	176	1.49	1.22	435.69	242.75	535.62	199.95	273.75	151.13	1.89	2.22

* Significant @ P = 0.05;   ** Significant @ P = 0.01 C_1: HA 10-8 × RIL 3-180; C_2: FPB 21 × RIL 3-180

TABLE XII

Estimates of additive genetic variance (σ^2_A) and dominance genetic variance (σ^2_D) for quantitative traits in F_4 populations derived from two crosses in dolichos bean

Traits	HA 10-8 × RIL 3-180		FPB 21 × RIL 3-180	
	σ^2_A	σ^2_D	σ^2_A	σ^2_D
Plant height (cm)	106.51**	72.22*	76.23**	81.95**
Primary branches plant^{-1}	0.03*	0.52	0.04**	0.99
Racemes plant^{-1}	0.78	10.96	0.69**	53.16**
Raceme length (cm)	1.65**	14.33**	0.24**	38.15**
Dry pods raceme^{-1}	0.11*	1.95	0.45**	0.30
Dry pods plant^{-1}	106.85**	36.85	50.02**	33.31
Dry pod weight plant^{-1} (g)	108.05**	14.55	51.09**	64.53
Dry seed weight plant^{-1} (g)	47.55**	36.22	43.33**	47.50
100 dry seed weight (g)	0.96**	0.25*	1.23**	0.18*

* Significant @ P = 0.05;   ** Significant @ P = 0.01

significant estimate of σ^2_D suggest the involvement of decreasing effect genes displaying directional dominance controlling raceme length in HA 10-8 × RIL 3-180. Selection in F_2 generations derived from three crosses may not be effective in improving genetic gain for plant height and raceme length as dominance and dominance × dominance (non-additive) gene effects are non-fixable. However, selection based on F_3 families is more effective as environmental variation is reduced by working with means and non-additive genetic variation is reduced by inbreeding. For the same reason, heritability of quantitative traits based on F_3 family means is greater than that based on F_2 individuals (Kearsey and Pooni, 1996). Perhaps one or two cycles of bi-parental mating in F_2 generation followed by recurrent selection is advisable with a twin objective of dissipating dominance and enhancing the frequency of genes with increasing effects on the expression of plant height and raceme length (Chandrakant *et al.,* 2015). Bi-parental mating offer additional opportunity for recombination and expression of new blocks of genes which allow the breeders to maximize the progress through selection (Hanson, 1959; Stam, 1977; Weber, 1982; Yonezawa, 1983). Non-significant [h] but significant σ^2_D was suggestive of the involvement of

genes with ambi-directional dominance controlling racemes plant^{-1} and raceme length in FPB 21 × RIL 3-180 and 100 dry seed weight in two crosses (HA 10-8 × RIL 3-180 and FPB 21 × RIL 3-180). Traits such as primary branches plant^{-1}, dry pods plant^{-1}, dry pod weight plant^{-1} and dry seed weight plant^{-1} appeared to be controlled by genes displaying no dominance or low dominance as indicated by non-significant/ significant small [h] and non-significant σ^2_D. Simple selection is expected to be effective for genetic improvement of above traits.

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TABLE XIII

Combination of first- and second degree statistics-based genetics of quantitative traits in dolichos bean

Traits	HA 10-8 × RIL 3-180				FPB 21 × RIL 3-180			
	First degree statistics		Second degree statistics		First degree statistics		Second degree statistics	
	Additive genetic effects(d)	Dominance genetic effects (h)	σ^2_A	σ^2_D	Additive genetic effects (d)	Dominance genetic effects (h)	σ^2_A	σ^2_D
Plant height (cm)	-9.30**±2.18	13.21**±2.14	9.55**	72.22*	-9.58**±1.52	14.07**±3.22	41.38**	81.95**
Primary branches plant⁻¹	0.14±0.15	0.60**±0.21	0.01**	0.52	0.66** ± 0.53	1.84** ± 0.19	0.13**	0.99
Racemes plant⁻¹	-1.33** ± 0.53	5.89 ***± 0.67	2.30**	10.96	-0.26±0.53	1.40**±0.66	2.92**	53.16**
Raceme length (cm)	-0.30 ± 0.23	2.62** ± .477	0.02	14.33**	-4.44**±0.60	6.81**±0.84	0.29*	38.15**
Dry pods raceme⁻¹	-0.17±0.19	3.28**±0.33	0.03	1.95	-3.21**±0.133	-0.82*±0.37	0.12	0.30
Dry pods plant⁻¹	-7.90**±2.18	25.73**±2.68	44.34**	36.85	-5.70***±1.89	28.62**±3.30	38.05**	33.31
Dry pod weight plant⁻¹ (g)	-8.26** ± 1.94	23.77** ± 3.71	43.58**	14.55	-10.68**± 1.63	19.64*** ± 3.01	50.14**	64.53
Dry seed weight plant⁻¹ (g)	-6.34** ± 2.3	23.01** ± 4.09	22.32**	36.22	-7.88**± 1.54	15.97** ± 2.69	43.11**	47.50
100 dry seed weight (g)	-1.73*** ± 0.143	2.99*** ± 0.36	0.10**	0.25*	-1.91*** ± 0.16	2.53** ± 0.34	0.01**	0.18*

* Significant @ P = 0.05;   ** Significant @ P = 0.01

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