Generation mean analysis for yield components in common bean

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Abstract

In order to choose an efficient breeding procedure, it is necessary to have knowledge of the genetic system controlling agronomically important traits. Common bean is one of the major legumes containing large amount of proteins and other valuable nutrients. The aim of this study was to determine genetic parameters for yield and yield components, using six generations (P1, P2, F1, F2, BC1, and BC2) derived from DERAKHSHAN×AND1007 and GOLI×D81083 crosses of common bean. A field experiment for these six generations was carried out in a randomized complete block design with three replications. The measurements included seed yield, pod weight, pod number per plant, seed number per pod, seed number per plant, and 100 seed weight. Generation mean analysis with three-parameter genetic model showed inadequacy of additive-dominance simple model to illustrate the genetic mechanism of the evaluated traits. Significant differences for two or more individual scaling tests (A, B, C, and D) in both crosses were recorded. Hayman six parameters genetic model suggested that both dominance and epistasis effects were important for most of the evaluated traits. Furthermore, expression of some traits in both crosses was affected by additive gene effects. Broad sense heritability was high for all traits except 100 SW in DER ×A1007 cross. Estimation of narrow sense heritability range was moderate for most traits. For SY and traits where portion of non-additive gene effect was higher, it is possible to exploit heterosis using the plant materials in this study.

Keywords: generation mean analysis; heritability; yield; common bean

Abbreviations:
GT: growth type; h_b^2: broad sense heritability; h_n^2: narrow sense heritability; IP: Introduced Place; MT: maturity time; PNPP: pod number per plant; PW: pod weight; SC: seed colour; SNPPL: seed number per plant; SNPP: seed number per pod; SS: seed size; SY: seed yield; 100 SW: 100 seed weight

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Introduction

An understanding of the mode of gene action, knowledge of genetic variances, levels of dominance, and the importance of genetic effects may help plant breeders to enhance yield potentials (Wolf and Hallauer, 1977). The genotypic mean of any population is affected by epistatic effects involving genic combinations of fixed and non-fixed genes. Estimation of these

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effects makes it possible to define specific additive × additive and additive × dominant epistatic components. Since such components cannot be easily determined, their importance cannot be assessed (Singh et al., 2006).

Generation mean analysis is one of the genetic models which is developed for the estimation of different genetic effects (Kearsey and Pooni, 2004;Checa et al., 2006; Tiruneh Mulugeta et al., 2013). This method could be used to partition the phenotypic variance to its components, i. e., genotyping, environmental, and genotype × environment components. Although plant breeders are kin to guess different component of phenotypic variance and consequently heritability, it is always difficult to predict heritability of a trait beforehand.

In order to determine genotypic values of the individuals and consequently mean genotypic values of families and generations, researchers use generation mean analysis to estimate the relative importance of average effects of the genes (additive effects), dominance deviations, and effects due to non-allelic genic interactions (Viana, 2000). It is possible to use basic generations to provide powerful tests of the adequacy of a simple genetic model and in particular, complex effects such as epistasis, maternal effects, etc. (Kearsey and Pooni, 2004). Such a model also provides the opportunity to determine the presence or absence of epistasis and measure them appropriately. Generation mean analysis also can detect the components of heterosis in terms of gene effects (Rebetzke et al., 2006; Farshadfar et al., 2001).

Common bean has great importance for developing countries. It provides protein and other valuable nutrients. Unfortunately, common bean yield and seed content quality are low in such communities. Simulation of SY of field crops, especially in common bean is a complex phenomenon made up of the interaction between different yield components and environmental effects (Misra et al., 1994), thus direct selection to improve this trait is not often effective. It is well-known that the efficiency of selection mainly depends on additive genetic variance, environmental effects, and genotype × environment interactions. As a result, to improve common bean yield in particular, breeding programs have to focus on sound genetic knowledge controlling yield and yield components. One research study showed that both additive and non-additive gene actions were important in the inheritance of number of seeds per pod in bean; whereas only additive type of gene action was important in the inheritance of 1000-seed weight (Tiruneh Mulugeta et al., 2013). Another study indicated that additive components and epistasis ([i], [l]) components play a major role in inheritance of resistance to common bean mosaic virus. Results of this study showed that additive gene effect has higher influence than other components. Therefore, selection for high resistance could be effective to modify this trait (Kamelmanesh et al., 2008).In order to perform genetic analysis of earliness in chickpea using generation mean analysis, an experiment was carried out to determine gene action for different traits including 100-seeds weight, number of pods per plant and SY of chickpea, and showed presence of high amount of dominant effect and dominant × dominant interactions that suggests the importance of non-additive genetic effects for these traits. Thus, selection in early generations for these traits could not be effectively successful (Karamiet al., 2011).

Heritability of metric characters has been widely used to assess the degree to which a character is transmitted from one parent to the offspring. This genetic component has been identified as a genetic relationship between the parents and offspring. It could provide information to indicate the possibility and the extent to which improvement in a character is possible. It could also be used to determine the proportion of heredity and environment in the expression of a trait (Adeniji, 2003). In a study on heritability and correlation of some traits in common beans, large heritabilities estimated for all traits was seen; therefore, direct empirical selection for yield should result in reasonable genetic gain from crosses among superior parents in a breeding program (Scullyl et al., 1991).

The aim of the present study was to perform genetic analysis of yield and yield components in common bean, using generation mean analysis. Furthermore, inheritance of traits under investigation was studied.

Materials and Methods

The experimental materials consisted of six generations (P1, P2, F1, F2, BC1, and BC2) derived from two crosses between (A1007 (P1) ×DER (P2)) and (GOLI (P1) ×D81083 (D81) (P2)) (Table 1). These six families are often referred to as the six basic generations (Kearsey and Pooni, 2004).

The parental lines were chosen primarily based on their difference in SY, yield components, and other traits. The parents (P1 and P2), first generation progenies (F1), second generation progenies (F2), first back cross progenies (P1×F1 = BC1), and second back cross progenies (P2×F1 = BC2) were evaluated in a Randomized Complete Block Design (RCBD)with 3 replications in the research field of Razi University, Kermanshah, Iran (latitude 34°19´ N, longitude 47° 7´E, and altitude 1322 m) in 2010.Each plot for various generations was sown in 3 rows. Each row was three meters long with a between-row spacing of 50 cm and a within-row spacing of 10 cm. The number of analyzed plants per plot varied depending on the generations.

Before sowing, 50 Kg ha^{-1} N fertilizer was applied. The field was irrigated every five to seven days. Weeds were removed whenever appeared.

Table 1 Characteristics of the cultivars used in this study

Cultivar	Characteristics					
	IP	Origin	MT	SS	GT	SC
AND1007	CIAT	Andian	Late	Large	indeterminate	Dark red
DERAKHSHAN	CIAT	Andian	Early	medium	determinate	Bright pink
GOLI	IRAN	Mesoameric	Late	medium	indeterminate	Dark red
D81083	CIAT	Andian	Early	Large	determinate	Red

Table 2 Analysis of variance for all traits in common bean

SOV	df	Mean squares					
		SY	PW	PNPP	SNPP	SNPPL	100 SW
Replications	2	86.19	223.28	159.23	0.292	173.16	9.42
Generations	11	639.83^{**}	1233.26^{**}	1014.23^{**}	1.97^{**}	1799.05^{**}	415.88^{**}
Error	22	37.93	69.61	65.23	0.158	170.54	5.31
C.V. (%)		16.84	14.18	16.75	11.01	9.76	7.44

The measured traits included SY, PW, PNPP, SNPP,SNPPL, and 100 SW. The measurements were done according to the Iinternational Board for Plant Genetic Resources (IPGRI)descriptor list for *P. vulgaris* L. (Anonymous, 1982).

Statistical analysis

Analysis of variance and mean comparison was done using MSTAT-C software. The three-parameter genetic model (Model 1, Mather and Jinks, 1982) was used for generation mean analysis. This model contains three parameters: mean, additive, and dominance gene effects. To test the adequacy of the model, the residual error sum of squares was tested for goodness of fit usingχ^2. The significance of each estimation was tested by t-test. In addition to this model, the individual scaling tests of Mather (1949) and Hyman and Mather (1955) were employed to test their fitness to the additive-dominance model. In case of the inadequacy of the three-parameter genetic model and significance of scaling tests, six-parameter genetic model suggested by Hyman (1958) was used to estimate various genetic components, assuming the absence of linkage, multiple alleles, lethal genes and full viability of gametes and zygotes. The components of F2 variance, i.e., the additive genetic variance (D), dominance variance (H), environmental variance

(EW), and correlation between D and H over all loci (F) were calculated by the following formula:

$$D = 2V_{F_2} - \left(V_{BC_1} + V_{BC_2}\right)$$
$$H = \left(V_{BC_1} + V_{BC_2}\right) - V_{F_2} - V_E$$
$$E_W = (V_{P_1} + V_{P_2} + V_{F_1})/3$$
$$F = V_{BC_1} + V_{BC_2}$$

The dominance ratio was estimated as H/D and were calculated according to Warner (1952) and Allard (1960) formulas.

Results

Table 2 shows the analysis of variance results for all traits. As it can be seen, there are significant differences among generations. As a result, generation means analysis of two crosses was further analyzed and relevant genetic parameters were calculated. The results of generation means and within plot variance for all traits revealed that variance estimates of the segregating generations were greater than that of

Table 3 Generation means± within plot variance for all traits in two crosses of common bean

Cross	Trait	Generations					
		P_1	P_2	F_1	BC_1	BC_2	F_2
(DER×A1007)	SY (gr)	20.29±0.42	31.15±1.36	31.18±0.25	37.43±9.02	31.96±9.08	45.27±9.56
	PW (gr)	36.91±2.80	52.19±1.44	51.38±0.35	62.58±18.43	58.92±18.29	68.51±17.79
	PNPP	28.56±1.45	30.94±1.54	31.33±1.35	52.50±14.24	52.85±16.56	45.62±14.58
	SNPP	2.21±0.01	4.61±0.01	4.27±0.01	3.18±0.02	3.22±0.02	4.01±0.02
	SNPPL	47.28±2.75	104.5±9.18	47.67±5.13	119.33±27.56	120.61±31.66	125.9±38.23
	100 SW	57.82±0.84	36.46±0.98	34.11±0.96	29.11±1.22	23.75±1.20	42.96±1.24
(GOLI×D81)	SY (gr)	45.73±1.21	25.70±1.78	27.47±1.72	31.44±6.21	47.77±8.70	46.08±8.79
	PW (gr)	70.95±2.87	39.45±2.45	40.44±3.80	53.23±13.36	71.12±13.58	69.92±12.82
	PNPP	63.72±5.74	31.56±1.75	41.06±6.42	47.06±9.58	56.06±13.61	64.14±14.01
	SNPP	4.59±0.01	3.83±0.02	3.41±0.02	3.40±0.03	4.49±0.02	3.77±0.03
	SNPPL	226.33±31.40	70.61±10.39	104.56±14.23	114.33±53.23	140.17±44.81	164.38±65.42
	100 SW	20.72±0.15	37.81±0.10	13.63±0.06	22.77±0.21	23.71±0.24	25.61±0.29

Table 4 Estimated values of three-parameter genetic model for all traits in two crosses of common bean

Cross	Trait	Parameters			
		[m] ±SE	[a] ±SE	[d] ±SE	χ^2
(DER×A1007)	SY	26.24±0.65**	5.50±0.66**	5.30±0.83**	43.24**
	PW	45.72 ± 1.01**	7.74 ± 1.01**	6.09 ± 1.18**	42.93**
	PNPP	31.08±0.85**	1.15±0.85 ns	2.66±1.44 ns	72.47**
	SNPP	3.28 ±0.07**	0.98 ±0.07**	0.75 ±0.11**	79.57**
	SNPPL	82.11 ±1.67**	30.67 ±1.67**	-22.08 ±2.82**	305.91**
	100 SW	44.58 ± 0.62**	-10.04 ± 0.62**	-16.05 ± 1.15**	258.99**
(GOLI×D81)	SY	36.92±0.84**	-8.65±0.84**	7.21±1.55**	71.88**
	PW	57.06 ±1.12**	-14.32 ± 1.13**	-10.95 ±2.20**	93.92**
	PNPP	48.16 ±1.30**	-15.02 ±1.30**	-1.93±2.73 ns	51.96**
	SNPP	4.33 ± 0.07**	-0.25 ±0.07**	-0.84 ±0.15**	39.97**
	SNPPL	146.92 ±3.03**	-69.46 ±3.04**	-37.55 ±4.92**	122.41**
	100 SW	30.16 ±0.23**	7.50 ±0.23**	-15.86 ±0.35**	181.71**

ns:not significant. ** Significant at the 0.01 probability level.

F_1 and their parents (Table 3). Three parameters estimation and the goodness of fit test of the model for all traits showed that [a] component was significant for all traits except PNPP in DER×A1007 cross, and [d] was significant for all traits except PNPP in both crosses (Table 4). As it is evident from Table 4, the χ^2 figure was significant in all cases and the additive-dominance model was inadequate for all traits. In this study, individual scaling tests for each trait showed that two to four individual scaling tests (A, B, C, and D) were significant in both crosses (Table 5). Six parameters model suggested by Hayman (1958) were used to estimate various genetic component values (Table 6). The results revealed that for SY in DER × A1007 cross, dominance [h], additive × additive [j], and dominance × dominance [l] genetic components of the mean were significant.

Table 5 A, B, C and D scaling for all traits in two crosses of common bean

Cross	Trait	Parameters			
		A	B	C	D
(DER×A1007)	SY	23.21±6.06**	1.59±6.16^{ns}	67.27±12.48**	21.24±7.51**
	PW	36.87±8.69**	14.27±8.73^{ns}	82.16±17.04**	15.51±10.39^{ns}
	PNPP	45.11±7.73**	43.43±8.31**	60.31±15.55**	-14.12±9.44**
	SNPP	-0.12±0.31^{ns}	-2.45±0.29**	0.70±0.58^{ns}	1.64±0.33**
	SNPPL	143.72±10.87**	89.05±11.87**	256.51±25.38**	11.87±14.57^{ns}
	100 SW	-33.72±2.59**	-23.08±2.60**	9.35±5.05^{ns}	33.07±2.72**
(GOLI×D81)	SY	-10.33±5.27*	42.36±6.19**	57.95±12.27**	12.96±7.08^{ns}
	PW	-4.94±7.75**	62.34±7.78**	88.39±15.02**	15.49**±8.4^{ns}
	PNPP	-10.67±7.10^{ns}	39.50±7.91**	79.18±16.04**	25.17±8.90**
	SNPP	-1.21±0.38**	1.74±0.36**	-0.18±0.73^{ns}	-0.36±0.4^{ns}
	SNPPL	102.22±16.1**	105.17±14.28**	151.47±33.84**	74.26±18.97**
	100 SW	-5.89±1**	13.07±1.08**	16.63±2.27**	4.73±1.27**

ns: not significant; * Significant at the 0.05 probability level; ** Significant at the 0.01 probability level.

Table 6 Estimated values of six-parameter genetic model for the studied traits in two crosses of common bean

Cross	Trait	Parameters				
		[m]	[d]	[h]	[i]	[j]
(DER×A1007)	SY	45.27±3.09**	5.38±4.26ns	37.02±15.04**	-42.47±15.01**	10.81±4.31**
	PW	68.51±4.22**	-7.64±1.03**	-4.08±0.47**	-31.03±20.77ns	11.30±6.15ns
	PNPP	45.62±3.82**	-0.35±5.55ns	29.82±18.94ns	28.23±18.88ns	0.84±5.62ns
	SNPP	4.01±0.13**	-0.04±0.19ns	-2.42±0.66**	-3.27±0.65**	1.16±0.20**
	SNPPL	125.90±6.18**	-1.28±7.70ns	-51.96±29.3ns	-23.74±29.1ns	27.34±7.89**
	100 SW	42.96±1.11**	5.36±1.56**	-79.17±5.56**	-66.14±5.43**	-5.32±1.70**
(GOLI×D81)	SY	46.08±2.97**	-16.3±3.86**	34.16±14.24**	-25.91±14.15ns	-26.34±3.96**
	PW	69.92±3.58**	-17.89±5.19**	-45.75±17.83**	-30.99±17.69ns	-33.64±5.32**
	PNPP	64.14±3.74**	-9±4.82ns	-56.93±18.03**	-50.35±17.80**	-25.08±5.01**
	SNPP	3.77±0.16**	-1.09±0.23**	-0.09±0.82ns	0.72±0.80ns	-1.48±0.24**
	SNPPL	164.38±8.09**	-25.83±9.90**	-192.44±38.3**	-148.52±37.9**	-103.69±10.4**
	100 SW	25.61±0.54**	-0.94±0.67ns	-25.10±2.57**	-9.46±2.54**	-9.48±0.72**

ns: not significant; ** Significant at the 0.01 probability level

As it can be seen, the additive [d], dominance [h], and additive × additive [j] components were significant for some traits in GOLI × D81 cross. For PNPP in DER × A1007 cross, only [l] component was significant whereas in GOLI× D81 cross, the components [h], [i], and [j] were significant.

Degree of dominance, variance components, h_b^2, and h_n^2 are presented in Table 7. The results showed that the additive variance was larger than dominance variance for SNPPL in both crosses, and for SY, PNPP, and 100 SW in GOLI × D81 cross. The ratio of √H/D in DER × A1007 cross for all traits except SNPPL showed over-dominance, whereas in GOLI × D81 cross for all traits except PW it displayed average dominance. Apparently,h_n^2 estimates were greater in magnitude than $h_n^2$for all traits in both crosses. Estimates ranged from 0.25 (100-seed weight) to 0.94 (SY) in DER × A1007 cross and from 0.54 (SNPP) to 0.85 (SY) in GOLI × D81 cross. Narrow-sense heritability ranged from 0.04 (100 SW) to 0.67 (SNPPL) in DER × A1007 cross and from 0.2 (PW) to 0.58 (PNPP) in GOLI × D81 cross. Moderateh_n^2 (0.2-0.5) was shown for 100 SW in DER × A1007 cross but other traits in both crosses revealed high (greater than 0.5) heritability (Stanfield, 2002).

Discussion

The opposite sign of [h] and [l] for PNPP and 100 SW in both crosses, SNPP in DER×A1007 cross and SY and SNPPL in GOLI×D81 suggested duplicate type of epistasis (Farshadfar et al., 2001; Zahravi, 1999). This complementary interaction increases the variation between the generations and in the segregation population. For other cases, the signs of the [h] were similar to the [l] type of epistasis, it was concluded that complementary type of interaction was present in the genetic control of these traits.

Additive effect [d] was found significant for PW in both cross, 100 SW in DER×A1007 cross and also for SY, SNPP, and SNPPL in GOLI×D81 cross. For other traits, additive effect [d] was not significant indicating that selection is not effective in early generation.

The genetic models fitted for SNPP trait in GOLI×D81 cross indicated the additive [d] and additive × dominance (j) gene effects. In the study by Tiruneh Mulugeta et al. (2013), additive and non-additive gene effects were important in controlling the inheritance of number of seeds per pod in common bean, but additive gene action was more important.

Additive × additive epistasis was significant for SY, SNPP, and 100 SW in DER× A1007 cross as well as for PNPP,SNPPL, and 100 SW in GOLI×D81 cross indicating the importance of this component and also suggesting an enhancing effect in the inheritance of these traits.

Table 7 Estimation of components of genetic variance for the studied traits in two crosses of common bean

Cross	Trait	Parameters								
		D	H	EW	F	√H/D	F/√D.H	h/d	h2b	h2n
(DER×A1007)	SY	75.59	113	12.16	-1.04	1.22	-0.01	1.01	0.94	0.38
	PW	86.41	259.66	27.58	2.61	1.73	0.02	0.89	0.93	0.23
	PNPP	57.92	217.95	30.28	-41.84	1.94	-0.37	1.33	0.92	0.19
	SNPP	0.10	0.10	0.17	0.04	1.02	0.35	0.71	0.56	0.27
	SNPPL	539.80	160.74	102.35	-73.74	0.55	-0.25	-0.99	0.88	0.67
	100 SW	0.15	0.78	2.78	0.07	2.25	0.20	-1.22	0.25	0.04
(GOLI×D 81)	SY	100.79	55.53	28.30	-44.82	0.74	-0.60	-0.82	0.85	0.55
	PW	53.29	161.17	54.68	-3.85	1.74	-0.04	-0.94	0.79	0.20
	PNPP	171.05	39.71	83.47	-72.59	0.48	-0.88	-0.41	0.72	0.58
	SNPP	0.19	0.12	0.26	0.10	0.79	0.68	-2.11	0.54	0.33
	SNPPL	982.96	54.80	336.09	151.50	0.24	0.65	-0.56	0.77	0.72
	100 SW	0.40	0.16	0.31	-0.09	0.64	-0.36	-1.83	0.65	0.46

Significance of [j] for SY, SNPP,SNPPL, and 100 SW in both crosses and PW and PNPP traits in GOLI×D81 cross revealed that selection through selfing (self-fertilization) is not effective for improvement of these traits (Farshadfar et al., 2001; Sharifi, 2005) because among the digenic interactions, additive × dominance type is more fixable and more useful for plant breeders (Sunil Kumar, 2005).

For all traits in both crosses (except PW in DER×A1007 cross and SNPP in GOLI×D81 cross) the contribution of dominance effect (h) is greater than additive effect. Therefore, dominance genes are the most important factors contributing to the genetic control of these characters. A negative estimate of dominance in some cases might be due to epistasic gene action in the cross-combinations.

A moderate heritability estimate may be attributed to the large environmental variations in F2 population. High estimate of h_n^2 shows that a large proportion of phenotypic variability for these characters was additive. This suggests that the selection in the early generations is worthwhile for genetic improvement.

Considering that h_n^2 was not low for any cases, it is concluded that environmental effects constitute a minor portion of the total phenotypic variation for these characters.

Conclusion

One advantage of generation mean analysis compared with other mating designs such as diallel is an increased level of sensitivity through a decreased error rate (Hallauer and Miranda, 1988). However, environmental differences may cause averages to cancel out effects for opposing directions. This may explain why the results of our experiment support the importance of non-additive effects such as dominance. In general, when quantitative characters are governed by additive or dominance gene action, hybrid breeding programs may be easily done. However, when interaction effects influence these characters, it becomes very difficult to improve characters by simple selection programs (Sunil Kumar, 2005). Our result also revealed that in comparison with the additive gene effects, dominance genes are the most important factors contributing to the genetic control of all traits (except PW in DER ×A1007 cross and SNPP in GOLI×D81 cross where additive gene effect was greater than dominant gene effect). Furthermore, epistatic components have also contributed to genetic variations of all traits (except PW in DER×A1007 cross that was controlled by additive and dominance gene action) in this study. Since additive gene effect was higher for SY, this may suggest the possibility of exploitation of heterosis effect for this important trait.

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