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Inheritance of primary yield component traits of common beans (*Phaseolus Vulgaris L.*): Number of seeds per pod and 1000 seed weight in an 8 × 8 diallel cross population

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Thirty six (36) genotypes (eight parents and 28 F_1 diallel crosses) were grown in randomized complete block design with two replicates during 2006 at Mandura, North western Ethiopia. The experiment was executed to study the inheritance of two primary yield component traits: number of seeds per pod and 1000 seed weight. Statistical significant difference was observed between genotypes, parents and crosses for the traits considered. The mean square due to general combining ability was significant for the two traits. However, specific combining ability mean square was significant only for number of seeds per pod. Thus, both additive and non-additive types of gene actions were important in the inheritance of number of seeds per pod. Significant b₁ component was obtained for number of seeds per pod. The b₂ and b₃ components however, were insignificant, suggesting the absence of gene asymmetry. From Wr/Vr graph, inheritance of seeds per pod was governed by partial dominance with additive gene action.

Key words: Diallel crosses, general combining ability, Phaseolus vulgaris L., specific combining ability.

INTRODUCTION

A common bean is rich in protein (20 to 28%), especially the amino acids lysine and tryptophan, and is an important source of minerals such as iron and zinc (MOARD, 2006; Ribeiro et al., 2007). It, therefore, supplements the cereal-based diet in many parts of the world. It is an important food crop in eastern and southern Africa, and recognised as the second most important source of human dietary protein and the third most important source of calorie of all the agricultural commodities produced in eastern and southern Africa (Kimani, 1999). In Ethiopia, common bean is one of the most important cash crops and source of protein for farmers. The country's export earnings is estimated to be over 85% of export earnings from pulses, exceeding that of other pulses such as lentils, horse (faba) bean and chickpea (Negash, 2007). Overall, common bean ranks third as an export commodity in Ethiopia, contributing about 9.5% of total export value from agriculture

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Abbreviations: ANOVA, Analysis of variance; GCA, general combining ability; SCA, specific combining ability.

Parent	Status/origin	Seed color	Seed shape	Seed size	Growth H
Roba-1	Released-1990	Cream	Elongated	Small	II
Dimtu	Released-2003	Red	Round	Small	П
Zebra	Released-1999	Carioca	Round	Medium	П
MAM-41	Released-2003	Cream	Round	Medium	III
BELDAK	CIAT	Cr. Pinto	Round	Medium	III
SK 93263	CIAT	White	Round	Medium	III
Tabor	Released-1999	Cream	Elongated	Medium	П
Red wolayta	Released-1974	Red	Elongated	Medium	П

Table 1. Description of the parents for the 8×8 diallel crosses of common bean.

BELDAK, BELDAKMI RR 5; Cr. Pinto, cream pinto; Growth H, growth habit; I, determinate bush; II, indeterminate prostrate. Seed size based on 100 seed weight: 1 to 24 g = small seed; 25 to 39 g = medium seed; 40 g and above = large seed.

(FAOSTAT, 2010). As legume, common bean improves soil fertility through biological nitrogen fixation. It is also one of the major crops preferred and produced in areas with short rainy season as it takes short days to mature, and is suitable for intercropping and double cropping (Legesse et al., 2006).

The choice of promising genotypes from diverse genetic base and their subsequent utilization for hybridization is one of the strategies for improving the productivity of crops including beans. A systematic study of the F₁ hybrids and their behavior in subsequent generations of selfing can generate basic genetic information about the type of gene action governing the inheritance of quantitative traits, and effective selection for seed yield and its components requires information on the magnitude of useful genetic variance present in the population (Esmail, 2007). However, the Ethiopian bean improvement program has focused on screening of introductions and could not generate basic genetic information and, hence, it is necessary to systematically test the performance of parental lines and their F_1 hybrids to generate the basic genetic information required for effective bean breeding program. A suitable genetical design is, the use of diallel mating system (Machado et al., 2002; Silva et al., 2004), a method where the progeny performance can be statistically separated into components relating to General Combining Ability (GCA) and specific combining ability (SCA) (Cruz et al., 2004; Glover et al., 2005). GCA and SCA are a measure of additive and non-additive genetic variation of parents and crosses, respectively (Sprague and Tatum, 1942).

Inheritance studies of important agronomic traits of different crops including common beans (Dhliwayo et al., 2005; Gwata et al., 2005; Jaramillo et al., 2005; Derera et al., 2007; Vidigal et al., 2008) have been conducted in various parts of the world. However, little information is available in Ethiopia. The study was, therefore, designed to generate basic genetic information on the inheritance of two important primary yield component traits of common beans: number of seeds per pod and 1000 seed weight.

MATERIALS AND METHODS

The experiment was conducted at Mandura, Metekel zone, Benishangul Gumuz regional state, North-western Ethiopia. Thirty six genotypes (eight parents and their 28 F₁ diallel crosses) were studied in two replicates of randomized complete block design in 2006. Diallel crosses were made by hand and plants were hybridized using emasculation with protected stigma method: the flower bud of the female parent is emasculated, sepals are kept intact to protect the bud, and pollination quickly follows (CIAT, 1977), at Melkassa Agricultural Research Center in the central rift valley of Ethiopia during the dry season (March to June, 2005) under furrow irrigation and during the rainy season (July to September, 2005) to ensure enough F1 seed for planting. Six of the parents were released varieties and being under production in different agro ecologies of Ethiopia and two CIAT lines (BELDAKMI RR5 and SK93263) were screened at Awassa College of Agriculture for good performance. Description of the eight parents used in the diallel cross study are given in Table 1. A plot consisting of two 1 m long rows spaced 60 cm apart was used to facilitate furrow supplemental irrigation when needed. Intra-row plant-to-plant spacing was 10 cm. Two seeds were hand planted per hill and the stand thinned to one plant per hill 10 days after emergence to maintain 20 plants per plot. Standard agronomic and plant protection treatments were used uniformly across the plots for the duration of the experiment.

A random sample of five plants from each plot and a random sample of five pods from each of the five plants were selected to collect data on number of seeds per pod; whereas, 1000 seed weight was measured on plot bases. The data were subjected to the analysis of variance (ANOVA) using SAS statistical software (SAS, 2004). Existence of significant difference among genotypes justifies further analysis. Diallel analysis was carried out according to Griffing (1956) Method II, Model I (fixed model), which involves parents and one-way F1 hybrids. Griffing's diallel analysis was supplemented by Hayman (1954) analysis. Combining ability analyses were carried out using a SAS program developed by Zhang and Kang (1997). The (Wr/Vr) ANOVA and graphs are the other powerful tools in Hayman's analysis with an inbuilt test for epistasis. In the absence of epistasis, the regression of Wr on Vr gives a linear regression line of unit slope. Therefore, the deviation of this regression line from unity is an indication of the existence of epistasis. Direct ANOVA of (Wr - Vr) also tests the absence/presence of epistasis. Significance of the difference (Wr-Vr) is an indication of the existence of epistasis. The intercept of the Wr/Vr regression line also shows the degree of dominance. If the regression line intercepts the Wr axis above the point of origin, this indicates incomplete dominance. If the regression line passes

Source	DF	Sum of squares	Mean square	F-value	Probability
Replication	1	6.902	6.902	31.36	0.0001
Genotype	35	42.139	1.204	5.47	0.0001
Parents	7	16.914	2.416	8.53	0.0056
Crosses	27	23.959	0.887	5.79	0.0001
AVHET	1	1.265	1.265	5.75	0.022
Error	35	7.703	0.22		
Total	71	56.744			
1000-seed weight					
Replication	1	34.7222	34.7222	0.07	0.7938
Genotype	35	153548.6111	4387.1103	8.77	0.0001
Parents	7	38743.7500	5534.8214	5.39	0.0205
Crosses	27	113050.0000	4187.0370	15.83	0.0001
AVHET	1	1754.8600	1754.8600	3.5067	0.06950
Error	35	17515.2778	500.4365		
Total	71	1710.986			

Table 2. Analysis of variance for number of seeds per pod and 1000 seed weight.

AVHET, Average heterosis; DF, degree of freedom.

through the origin, then there is complete dominance. If the intercept is negative (the regression line passes below the point of origin), then over dominance contributes to the expression of the trait. Finally, the correlation between parental means and the covariance (Wr) is used to judge the direction of dominance. If the correlation coefficient (r) is negative, dominance tends to increase the trait. If r is positive then dominance decreases the trait.

RESULTS AND DISCUSSION

Ordinary analysis of variance for the 36 genotypes was carried out according to Steel and Tore (1980), and there was significant difference between the genotypes for the traits studied: number of seeds per pod and 1000 seed weight. Parents also differed in these traits which show that there is enough additive genetic variance to be exploited. Similarly, statistical significant difference was observed between crosses for the traits (Table 2). Griffing's method II model I and Hayman's approach analysis of variance of diallel analysis are merged into one table without changing the essence of both the models. The mean square due to GCA was significant for the traits considered: number of seeds per pod and 1000seed weight. However, SCA mean square was significant only for number of seeds per pod. Thus, both additive and non-additive types of gene actions were important in the inheritance of number of seeds per pod; although, additive gene action was more important as the variance component due to GCA was greater than that due to SCA (the ratio of GCA: SCA variance component was more than unity and is 2.5, as indicated in Table 3). This result agrees with Islam et al. (2006), Hinkossa et al. (2013) in common bean and Idahosa and Alika (2013) in cowpea, but partially contradicts with Cruz et al. (2004) and Vidigal et al. (2008) where both found significant GCA and SCA mean squares with preponderance of SCA component in their genetic studies of common beans. Significant b_1 (average heterosis) component was obtained for number of seeds per pod indicating the presence of directional dominance in the expression of the trait. The b_2 and b_3 components however, were not significant, suggesting the absence of gene asymmetry in the parents and SCA effects in the crosses, respectively.

Evidence that both additive and non-additive gene effects are involved in the genetic control of the trait investigated implies that both gene effects should be considered when developing breeding schemes for the selection of superior lines. Consequently, both parents need not necessarily have high GCA during breeding because the dominance gene effects could also be exploited to enhance these traits. In contrast, the predominance of the additive gene effects suggests that the best progeny might be derived from crosses with genotypes having the greatest positive GCA (Arunga et al., 2010).

The study revealed only additive type of gene action was important in the inheritance of 1000-seed weight. It further suggested that genetic gain is feasible through selection over segregating population for the trait. This finding disagrees with many previous works which emphasized the importance of both additive and nonadditive types of gene actions for the inheritance of the trait (White et al., 1994; Vidigal et al., 2008).

The GCA and SCA effects of the traits are presented in

Source	DF	Sum of squares	Mean square	F-value	Probability
Genotype	35	42.1390	1.2040	5.4700	0.00010
GCA (a)	7	31.1461	4.4495	20.2156	0.00000
SCA (b)	28	10.9927	0.3926	1.7837	0.05256
b1	1	1.2650	1.2650	5.7500	0.02200
b2	7	2.0432	0.2919	1.3261	0.26744
b3	20	7.6842	0.3842	1.7456	0.07276
Error	35	7.7035	0.2201		
Ratio of GCA:SCA variance	e components: 2.4	497			
1000-seed weight					
Genotype	35	153548.6111	4387.1031	8.7700	0.00010
GCA (a)	7	141637.5000	20233.9286	40.4323	0.0001
SCA (b)	28	11911.1111	425.3968	0.8501	0.6681
b1	1	1754.8600	1754.8600	3.5067	0.06950
b2	7	3622.9200	517.5600	1.0342	0.42540
b3	20	6533.3300	326.6700	0.6528	0.84281
Error	35	17515.2778	500.4365		
Ratio of GCA:SCA variance	e components: 26	6.40			

Table 3. Griffing's method II model I and Hayman's diallel analysis for number of seeds per pod and 1000 seed weight.

GCA (a), General combining ability; SCA, specific combining ability; b_1 , tests overall difference between parental and F_1 means; b_2 , measures consistency of mean dominance deviation over arrays (gene asymmetry); and b_3 , measures non-additive deviations unique to each F_{1s} (SCA effects); DF, degree of freedom.

Table 4. Roba-1, Zebra, BELDAKMI RR 5, SK 93263 and Tabor had significant GCA effects for number of seeds per pod. Roba-1 and Tabor were good general combiners for the trait as they showed maximum GCA effects. Moreover, they had the highest per se performance and showed the maximum cross mean performances. The hybrids that showed the maximum number of seeds per pod involved Roba-1 and Tabor as one parent. This result is in good agreement with previous works studied on common beans (Foolad and Bassiri, 1983; Rainey and Griffith, 2005). The character is one of the principal yield components in common bean (Dursun, 2007; Salehi et al., 2010; Cokkizgin et al., 2013). Hence, these two parents could be considered as good parent for future hybridization programme with a major aim of improving yield.

Parents, SK 93263 and BELDAKMI RR 5 on the other hand exhibited the minimum GCA effects for the trait, suggesting that these two parents were poor combiners for number of seeds per pod in their progenies. All parents except Zebra exhibited highly significant GCA effects for 1000-seed weight. SK 93263 followed by BELDAKMI RR 5 were good general combiners for the trait and had highest per se performance. However, these two parents were poor general combiners for number of seeds per pod. Similarly, Roba-1 which was a good general combiner for number of seeds per pod here exhibited the minimum GCA effect. The correlation between the two traits (r = -0.73, p = 0.01) was significantly negative confirming the aforementioned result. A similar result on common bean has been published by Balcha (2010). Generally, none of the parents exhibited positive and/or negative significant GCA effect for both of the traits considered. Such situations could possibly be explained by the phenomenon of component compensation in beans (Adams, 1967). Information on SCA estimates of crosses are important to know the hybrid performance based on the per se performance of parental lines. This is practically relevant when the SCA mean square is statistically significant and hence only SCA effects of number of seeds per pod which showed significant SCA mean squares are presented. Only six crosses exhibited significant SCA effects for number of seeds per pod, among which five crosses (Roba-1 x SK 93263, BELDAKMI RR 5 x Tabor, SK 93263 x Tabor, BELDAKMI RR 5 x Red wolayta and Tabor x Red wolayta) showed positive SCA effects for the trait, indicating that these crosses produced larger number of seeds per pod than it would be expected from the per se performance of the parents.

Different statistics and their significance tests of the Hayman's graphical approach for number of seeds per pod are presented in Table 5. The Wr/Vr graph for number of seeds per pod (Figure 1) revealed that the estimated regression line intercepted the Wr-axis above the point of

Numbe	er of seeds p	er pod								
	1	2	3	4	5	6	7	8	Cr.M	GCA
1	-0.075	5.400	5.390	4.800	5.080	5.420	5.720	5.070	5.270	0.78**
2	-0.100	0.021	4.770	4.980	4.640	3.870	4.330	4.870	4.692	0.14
3	0.311	0.331	-0.033	4.120	3.600	3.520	4.540	4.480	4.345	-0.28*
4	-0.370	0.445	0.014	-0.078	3.760	3.880	5.230	4.300	4.437	-0.19
5	0.182	0.383	-0.234	-0.169	-0.874	4.000	5.180	4.760	4.432	-0.46**
6	0.63*	-0.281	-0.209	0.056	0.451	-0.407	5.210	3.550	4.208	-0.57**
7	-0.159	-0.9**	-0.278	0.323	0.55*	0.68*	-0.362	5.680	5.129	0.52**
8	-0.340	0.095	0.130	-0.142	0.59*	-0.510	0.53*	-0.175	4.674	0.05
P.M	6.070	4.880	3.980	4.120	2.780	3.040	5.260	4.510		
1000-s	eed weight									
	1	2	3	4	5	6	7	8	Cr.M	GCA
1	0.889	225.00	245.00	270.00	265.00	265.00	205.00	200.00	239.28	-35.4**
2	17.389	-1.111	240.00	260.00	270.00	300.00	235.00	200.00	247.14	-26.9**
3	4.889	-8.611	-16.11	310.00	335.00	330.00	260.00	235.00	279.28	5.625
4	7.889	-10.61	6.889	-20.11	330.00	375.00	270.00	280.00	299.28	27.6**
5	0.389	-3.111	29.39*	2.389	-25.11	360.00	290.00	270.00	302.85	30.1**
6	-16.61	9.889	7.389	30.39*	12.889	-19.11	285.00	295.00	315.71	47.1**
7	-8.611	12.889	5.389	-6.611	10.889	-11.11	-3.111	225.00	252.85	-20.9**
8	-7.111	-15.61	-13.11	9.889	-2.611	5.389	3.389	9.889	243.57	-27.4**
P.M	200.00	215.00	265.00	305.00	305.00	345.00	225.00	225.00		

Table 4. Estimation of GCA and SCA effects and actual parent and cross values for number of seeds per pod and 1000 seed weight.

Diagonals and below the diagonals represent SCA effects and above the diagonals represent the actual values of the crosses in grams; GCA, General combining ability effects of the parents; P. M, the per se of the parents; Cr. M, cross mean of every parent; *, ** represent significant of GCA and SCA effects from zero at P \leq 0.05 and 0.01, respectively; 1 = Roba-1; 2 = Dimtu; 3 = Zebra; 4 = MAM-41; 5 = BELDAKMI RR 5; 6 = SK93263; 7 = Tabor; 8 = Red wolayta.

Table 5. Different statistics for the Hayman's graphical approach of diallel analysis.

Number of seeds per pod							
Parent	Vr	Wr	(Wr+Vr) [*]	(Wr-Vr) ^{ns}			
Roba-1	0.244	0.286	0.530	0.041			
Dimtu	0.303	0.363	0.666	0.060			
Zebra	0.594	0.773	1.367	0.179			
MAM-41	0.365	0.479	0.844	0.113			
BELDAKMI RR 5	0.800	0.759	1.559	0.042			
SK 93263	0.729	0.692	1.421	0.037			
Tabor	0.275	0.110	0.385	0.165			
Red wolayta	0.550	0.400	0.950	0.150			
$b_{Wr,Vr} = 0.96^{ns}$		Intercept = 0.11 ^{ns}					

Vr = Variance of all the progenies in each parental array (an array is a group of crosses involving a particular parents); Wr = covariance between parents and their offspring's in each array; $b_{Wr, Vr} = regression$ of Wr on Vr and test for $b_{Wr, Vr} = 1$, and intercept = the point where the regression line intercepted the Wr-axis test for intercept = 0.

origin. This suggested that inheritance of number of seeds per pod was governed by partial dominance with additive type of gene action. The regression line did not significantly deviate from unit slope, suggesting the absence of epistasis. The distribution of array points on the regression line indicated that, Tabor possessed the maximum number of dominant gene, being closest to the origin. BELDAKMI RR 5 on the other hand possessed the maximum recessive genes, being farthest from the point of origin.

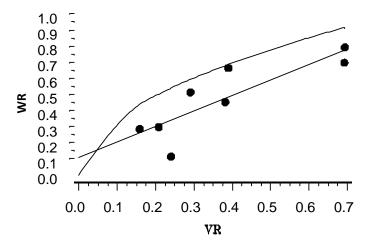


Figure 1. Wr/Vr graph for number of seeds per pod.

Array points was scattered along the regression line on the graph indicating the genetic diversity among parents for number of seeds per pod. The results found in the study in both Griffing's method II model I and Hayman's approach was in good agreement, and it agrees with previous findings on cowpea (Idahosa and Alika, 2013).

Conclusion and recommendation

Information on the genetic mechanism that governs the inheritance of quantitative characters has got a paramount importance in devising an effective breeding strategy. The present study was, therefore, executed to study the inheritance of two primary yield component traits: number of seeds per pod and 1000 seed weight in an 8×8 diallel cross population of common bean. In the 8×8 diallel crosses of elite common bean genotypes (6 released varieties and 2 promising genotypes); there was significant difference between genotypes, parents and crosses for the traits considered. Presences of significant statistical difference between parents show that there is sufficient additive genetic variance to be exploited. The crosses were in general superior in performance than parents, indicating presence of directional dominance which increases these traits. The result of the present study showed that only additive type of gene action was important in governing the inheritance of 1000 seed weight. However, both additive and non-additive types of gene actions were important in the inheritance of number of seeds per pod. Additive gene action was more important as the variance component due to GCA was greater than that due to SCA. This was further complimented by the graphical approach of Hayman where the inheritance of number of seeds per pod was governed by partial dominance with additive type of gene action. The preponderance of additive genetic variation in early generation would indicate higher heritability and the

possibility of identifying transgrassive practically homozygous genotypes. Conventional breeding methods like recurrent selection and pedigree selection could be employed to improve such traits.

Roba-1 proved to be good general combiner and possessed more number of dominant genes for number of seeds per pod. Moreover, it has got the maximum per se performance for the trait. Similarly, Tabor was good general combiner and possessed more number of dominant genes for the same trait and also it has been involved as one parent for the crosses that exhibited the maximum SCA effects for number of seeds per pod and 1000-seed weight. Thus, these varieties could be considered as a good parent for future common bean hybridization programme.

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