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Genetic Diversity, Correlation and Path Analysis Studies in Landraces of Faba Bean (*Vicia faba L.*)

Riya Thakur[1], Pragyan Adhikari[1] and Gopal Katna[2]*

[1]Department of Genetics and Plant Breeding, Chaudhary Sarwan Kumar Himachal Pradesh Krishi Vishvavidyalaya, Palampur - 176062, Himachar Pradesh, India
[2]Department of Organic Agriculture and Natural Farming, Chaudhary Sarwan Kumar Himachal Pradesh Krishi Vishvavidyalaya, Palampur - 176062, Himachar Pradesh, India; gkatna@gmail.com

Abstract

The present study was conducted using 35 faba bean genotypes in a randomised block design with three replications for yield and nutritional traits. Significant differences among genotypes were observed for the studied traits. High heritability and moderate genetic advance were recorded for 100-seed weight and protein. The branches per plant, pod length, pods per node, pods per plant, seeds per pod, biological yield, harvest index and 100-seed weight showed significant positive associations with seed yield at both phenotypic and genotypic levels. Path analysis highlighted biological yield and harvest index as the most important traits due to their positive direct effects on seed yield at phenotypic and genotypic levels. The D^2 analysis classified genotypes into eight clusters, with the maximum in Cluster III (16). The presence of a high inter-cluster distance between cluster II (containing genotypes RFB-41, HPFB-20-13, HPFB-20-16, RFB-39 and RFB-42) and cluster V (containing the genotype HPFB-20-06) (20.68) also suggested considerable potential for exploiting heterotic effects through hybridisation among genetically diverse parents.

Keywords: Correlation, D^2 Analysis, Genetic Diversity, Path Analysis, *Vicia faba*

Faba bean (*Vicia faba* L.) is an often-cross-pollinated crop (2n=2x=12) belonging to the *Fabaceae* family. It is grown in mid and low hill regions of Himachal Pradesh and is vital from ecological, nutritional and economic points of view[1]. Faba bean seeds are a good source of protein that ranges from 20 to 41% due to varietal differences[2] besides containing micronutrients and dietary minerals mainly potassium, phosphorus, iron and zinc[3]. It has multi-purpose benefits as food and fodder like hay, silage and straw. The fresh, young, and tender pods are used as a green vegetable, while mature seeds can be consumed in various ways, such as whole or ground into flour.

The selection and widespread cultivation of a narrow range of high-yielding faba bean varieties have contributed significantly to increased global production. However, this uniformity and selection for specific traits have caused a decline in genetic diversity due to limited variation among existing cultivated varieties[4]. To facilitate further improvement in faba bean, the enhancement of genetic diversity is the primary aim of breeding programs. The existence of genetic diversity in crop plant species permits the breeders to select desirable genotypes either directly as a new variety or involve hybridisation programmes as parents[5,6]. Therefore, the present study on genetic

*Author for correspondence

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diversity would be significant to identify the valuable characters for developing varieties with improved traits[7].

MATERIALS AND METHODS

The experimental material for the present study comprised 32 faba bean genotypes and 3 checks (Vikrant, HFB-1 and HFB-2). The genotypes along with checks were tested for various agro-morphological traits in a randomised block design during *Rabi*, 2022-23 at Integrated Research Farm Holta, Department of Organic Agriculture and Natural Farming at CSKHPKV, Palampur, with a plot size of 2 m x 20 cm with row to row and plant to plant distance of 30 cm and 10 cm, respectively. Observations were recorded on 14 agro-morphological traits namely, days to flowering, days to maturity, plant height (cm), branches per plant, flowers per inflorescence, pod length (cm), pod width (cm), pods per node, pods per plant, seeds per pod, biological yield per plant (g), harvest index (%), 100-seed weight (g) and seed yield per plant (g) and also on protein content (%). The data for different characters were analysed as per the standard procedure suggested by Panse and Sukhatme[8]. Estimates of coefficients of variation (genotypic, phenotypic and environmental) were worked out using formulae of Burton and DeVane[9]. Broad sense heritability (h^2bs) as per Burton and DeVane[9], Genetic Advance (GA) as suggested by Johnson *et al.*[10], correlation coefficients (phenotypic and genotypic) following Al-Jibouri *et al.*[11], and direct and indirect path coefficients using Dewey and Lu[12] method were calculated. The D^2 analysis was carried out as per the procedure given by Mahalanobis[13]. D^2 values were used to group the different genotypes into various clusters following Tocher's method as suggested by Rao[14]. Protein content was estimated by the Micro-Kjeldahl method.

RESULTS AND DISCUSSION

The analysis of variance (Table 1) showed significant differences for all the traits, signifying wide variation among genotypes. The higher values of Phenotypic Coefficient of Variation (PCV) for all studied traits as compared to corresponding Genotypic Coefficient of Variation (GCV) suggest the influence of environmental factors on the manifestation of genotypes.

The information on heritability impacts the choice of breeding procedures to envisage gain from selection and to regulate the comparative importance of genetic effects. The extent of heritability assumes the consistency to identify genotypes through their phenotypic appearance that aid to envisage possible degree of improvement together with the genotypic coefficient of variation[16]. High heritability estimates (>80%) for days to flowering, pod length, 100-seed weight and protein content were observed, while moderate estimates were recorded for days to maturity, plant height, branches per plant, flowers per inflorescence, pod width, pods per node, pods per plant, seeds per pod, biological yield per plant, harvest index and seed yield per plant (50-80 %), signifying that these traits were not much influenced by environmental conditions. Similar heritability levels have been reported by various researchers in their respective studies for days to 50% flowering by Sheelamary and Shivani[17], number of branches per plant by Alghamdi[18], and plant height by Toker[19]. However, high heritability does not principally mean high genetic gain and is insufficient to expect development simply through phenotypic selection[20,21]. It is therefore beneficial to work out genetic advance along with heritability.

Moderate genetic advance (25-50 %) was detected for pod width, pods per node and seed yield, while other traits showed low values (<25%). Similar findings have also been reported by Sheelamary and Shivani[17]. High heritability accompanied by moderate genetic advance was observed for 100-seed weight and protein, suggesting the preponderance of additive gene action in the manifestation of these traits that support direct selection for their improvement[22].

Table 1. Analysis of variance and genetic parameters for agro-morphological and quality traits

Traits	Replication	Treatment	Error	PCV (%)	GCV (%)	h^2_{bs} (%)	Expected GA
Degrees of freedom (df)	2	34	68				
DTF	12.01	66.58*	3.61	5.37	4.96	85.42	9.45
DTM	36.61	31.22*	5.51	2.31	1.8	60.64	2.89
PH	28.22	37.64*	5.2	8.33	6.84	67.54	11.59
NBP	0.8	0.29*	0.05	17.3	13.17	57.9	20.64
NFI	0.28	0.57*	0.09	18.82	14.72	61.23	23.74
PL	0.01	0.95*	0.07	13.52	12.1	80.15	22.32
PW	0.06	0.17*	0.01	23.21	20.72	79.64	38.09
NPN	0.2	0.51*	0.05	17.82	15.53	75.96	27.89
NPP	5.48	11.80*	1.78	9.57	7.69	64.63	12.74
NSP	0.12	0.42*	0.08	15.18	11.67	59.06	18.48
BY	16.15	92.99*	7.88	12.56	11.1	78.19	20.23
HI	33.39	50.61*	7.48	12.8	10.16	62.91	16.06
HSW	1.35	103.99*	1.94	15.99	15.55	94.59	31.16
PC	7.48	20.21*	0.38	14.17	13.27	87.69	25.6
SY	18.05	32.80*	1.13	21.39	18.99	78.86	34.75

*Significant at 5% level of significance; PCV and GCV: Phenotypic and genotypic coefficient of variation, h^2_{bs}: Heritability in broad sense, GA: Genetic advance (%) of mean, DTF: Days to flowering, DTM: Days to maturity, PH: Plant height, NBP: branches per plant, NFI: flowers per inflorescence, PL: Pod length, PW: Pod width, NPN: pods per node, NPP: pods per plant, NSP: seeds per pod, BY: Biological yield, HI: Harvest index, HSW:100-Seed weight, PC: Protein content, SY: Seed yield per plant.

Correlation Studies and Path Coefficient Analysis

It is imperative to study the association of yield with other attributes vis-à-vis between themselves, that may constitute the basis to identify characters for both direct and indirect selection that pave the way to define an ideal plant type[23,24]. Phenotypic correlation analysis revealed that seed yield had significant positive correlations with biological yield, pods per plant, harvest index, 100-seed weight, pod length, seeds per pod, pods per node and branches per plant. A strong negative association of seed yield was observed with days to flowering and days to maturity, indicating higher yields can be obtained from early-maturing genotypes (Table 2). Genotypic correlation coefficients

Table 2. Estimates of phenotypic and genotypic correlation coefficients for agro-morphological and quality traits

Traits		DTM	PH	NBP	NFI	PL	PW	NPN	NPP	NSP	BY	HI	HSW	PC	SY
DTF	P	0.651*	0.006	-0.116	-0.004	-0.293*	0.036	-0.108	-0.763*	-0.241*	-0.579*	-0.649*	-0.495*	0.149	-0.795*
	G	0.884*	0.012	-0.161	0.009	-0.386*	0.044	-0.124	-0.965*	-0.343*	-0.701*	-0.855*	-0.540*	0.182	-0.940*
DTM	P		-0.029	0.032	-0.111	-0.284*	-0.173	-0.034	-0.623*	-0.183	-0.481*	-0.568*	-0.351*	-0.08	-0.652*
	G		-0.077	0.071	-0.155	-0.409*	-0.188	-0.104	-0.920*	-0.308*	-0.720*	-0.832*	-0.441*	-0.122	-0.908*
PH	P			-0.082	0.226*	0.189	-0.03	0.188	-0.001	0.046	0.317*	-0.126	-0.19	-0.08	0.14
	G			-0.093	0.310*	0.286*	0.024	0.274*	0.048	0.072	0.379*	-0.202*	-0.236*	-0.066	0.152
NBP	P				0.039	-0.113	0.162	0.122	0.162	0.263*	0.221*	-0.093	0.053	-0.194*	0.142*
	G				0.019	-0.157	0.178	0.200*	0.195*	0.516*	0.282*	-0.069	0.07	-0.304*	0.240*
NFI	P					0.17	-0.039	0.105	-0.033	-0.048	0.193*	-0.152	-0.098	0.036	0.047
	G					0.261*	-0.057	0.253*	-0.02	0.028	0.322*	-0.166	-0.139	-0.003	0.133
PL	P						-0.046	-0.006	0.266*	0.099	0.295*	0.229*	0.273*	-0.114	0.325*
	G						-0.028	-0.018	0.421*	0.176	0.337*	0.361*	0.329*	-0.119	0.393*
PW	P							-0.085	0.097	-0.078	0.057	0.025	0.019	0.109	0.094
	G							-0.057	0.134	-0.061	0.114	-0.027	0.022	0.115	0.101
NPN	P								0.081	-0.088	0.234*	0.079	0.073	-0.166	0.207*
	G								0.145	-0.181	0.336*	0.005	0.089	-0.181	0.263*
NPP	P									0.17	0.580*	0.535*	0.350*	-0.035	0.702*
	G									0.327*	0.809*	0.937*	0.421*	-0.026	0.964*
NSP	P										0.162	0.200*	0.145	-0.242*	0.286*
	G										0.241*	0.279*	0.169	-0.318*	0.373*
BY	P											0.082	0.087	-0.153	0.735*
	G											0.346*	0.1	-0.154	0.910*
HI	P												0.511*	0.049	0.618*
	G												0.695*	0.086	0.714*
HSW	P													-0.284*	0.334*
	G													-0.295*	0.398*
PC	P														-0.091
	G														-0.06

*Significant at 5% level of significance; P: Phenotypic correlation coefficient; G: Genotypic correlation coefficient

also exhibited similar trends. Overall, the value of genotypic correlation coefficients was higher than phenotypic correlation coefficients, which indicates the relationships among the various traits due to genetic factors[25]. Similar findings were also reported by Badolay *et al.*[26] and Kalia and Sood[27].

Table 3. Estimates of path coefficients for agro-morphological and quality traits at phenotypic (P) and genotypic (G) levels

Traits		DTM	PH	NBP	NFI	PL	PW	NPN	NPP	NSP	BY	HI	HSW	PC	SY
DTF	P	0.010	0.000	-0.002	0.000	-0.004	0.002	-0.003	0.033	-0.017	-0.354	-0.324	0.026	0.001	-0.795*
	G	-0.647	0.001	-0.063	-0.001	-0.025	-0.006	0.006	0.155	0.073	-0.378	-0.448	0.079	-0.028	-0.940*
DTM	P	**0.016**	0.000	0.000	0.000	-0.004	-0.011	-0.001	0.027	-0.013	-0.294	-0.283	0.018	0.000	-0.652*
	G	**-0.732**	-0.003	0.028	0.019	-0.027	0.028	0.005	0.148	0.066	-0.388	-0.436	0.065	0.019	-0.908*
PH	P	0.000	**-0.006**	-0.001	0.000	0.002	-0.002	0.005	0.000	0.003	0.193	-0.063	0.010	0.000	0.140
	G	0.056	**0.044**	-0.036	-0.038	0.019	-0.004	-0.014	-0.008	-0.015	0.204	-0.106	0.035	0.010	0.152
NBP	P	0.001	0.000	**0.013**	0.000	-0.001	0.011	0.003	-0.007	0.018	0.135	-0.047	-0.003	-0.001	0.142*
	G	-0.052	-0.004	**0.389**	-0.002	-0.01	-0.026	-0.010	-0.031	-0.110	0.152	-0.036	-0.010	0.046	0.240*
NFI	P	-0.002	-0.001	0.001	**0.002**	0.002	-0.003	0.003	0.001	-0.003	0.118	-0.076	0.005	0.000	0.047
	G	0.113	0.014	0.007	**-0.122**	0.017	0.008	-0.013	0.003	-0.006	0.173	-0.087	0.020	0.000	0.133
PL	P	-0.005	-0.001	-0.001	0.000	**0.012**	-0.003	0.000	-0.011	0.007	0.180	0.114	-0.014	-0.001	0.325*
	G	0.300	0.013	-0.061	-0.032	**0.065**	0.004	0.001	-0.068	-0.037	0.181	0.189	-0.048	0.018	0.393*
PW	P	-0.003	0.000	0.002	0.000	-0.001	**0.066**	-0.002	-0.004	-0.005	0.035	0.012	-0.001	0.001	0.094
	G	0.137	0.001	0.069	0.007	-0.002	**-0.148**	0.003	-0.022	0.013	0.061	-0.014	-0.003	-0.018	0.101
NPN	P	-0.001	-0.001	0.002	0.000	0.000	-0.006	**0.026**	-0.003	-0.006	0.143	0.040	-0.004	-0.001	0.207*
	G	0.076	0.012	0.078	-0.031	-0.001	0.008	**-0.051**	-0.023	0.038	0.181	0.003	-0.013	0.028	0.263*
NPP	P	-0.010	0.001	0.002	0.000	0.003	0.006	0.002	**-0.043**	0.012	0.354	0.267	-0.018	0.000	0.702*
	G	0.674	0.002	0.076	0.002	0.027	-0.02	-0.007	**-0.161**	-0.070	0.436	0.491	-0.062	0.004	1.064*
NSP	P	-0.003	0.000	0.003	0.000	0.001	-0.005	-0.002	-0.007	**0.070**	0.099	0.100	-0.008	-0.001	0.286*
	G	0.226	0.003	0.201	-0.003	0.011	0.009	0.009	-0.053	**-0.213**	0.130	0.146	-0.025	0.049	0.373*
BY	P	-0.008	-0.002	0.003	0.000	0.004	0.004	0.006	-0.025	0.011	**0.610**	0.041	-0.005	-0.001	0.735*
	G	0.527	0.017	0.110	-0.039	0.022	-0.017	-0.017	-0.130	-0.051	**0.539**	0.181	-0.015	0.024	0.910*
HI	P	-0.009	0.001	-0.001	0.000	0.003	0.002	0.002	-0.023	0.014	0.050	**0.499**	-0.026	0.000	0.618*
	G	0.609	-0.009	-0.027	0.020	0.023	0.004	0.000	-0.151	-0.059	0.186	**0.524**	-0.102	-0.013	0.714*
HSW	P	-0.006	0.001	0.001	0.000	0.003	0.001	0.002	-0.015	0.010	0.053	0.255	**-0.052**	-0.001	0.334*
	G	0.323	-0.010	0.027	0.017	0.021	-0.003	-0.005	-0.068	-0.036	0.054	0.364	**-0.147**	0.045	0.398*
PC	P	-0.001	0.000	-0.003	0.000	-0.001	0.007	-0.004	0.001	-0.017	-0.093	0.025	0.015	**0.005**	-0.091
	G	0.089	-0.003	-0.118	0.000	-0.008	-0.017	0.009	0.004	0.068	-0.083	0.045	0.043	**-0.153**	-0.060

Residual effects (P) = 0.13369, Residual effects (G)=0.01031,*Significant at 5% level of significance; Bold values indicate direct effects

At the phenotypic level, positive and high direct effects were observed for biological yield per plant, followed by harvest index and seeds per pod, which contributed significantly to the positive association with

yield, while the majority of other traits exhibited their association due to positive indirect effects via biological yield, harvest index and pods per plant (Table 3). At the genotypic level, direct effect estimates were positive and high for biological yield per plant, harvest index, and days to 50% flowering (Table 3). However, days to 50% flowering showed a high negative correlation with seed yield per plant, suggesting that negative indirect effects of other traits play a major role in determining the correlation with yield at the genotypic level. Positive correlation of biological yield with seed yield was mainly the result of high positive direct effects and the indirect effect via days to maturity. These findings are comparable to those of Kumar *et al.*[28], Arya[29] and Kishore *et al.*[30]

Genetic Diversity Studies

Based on D^2 values, the 35 genotypes under study were grouped into eight clusters (Table 4). Cluster III was the largest, consisting of 16 genotypes, followed by cluster I with 9 genotypes and cluster II with 5 genotypes. Intra-cluster distances ranged from 0.00 to 9.64 (Table 5). The highest intra-cluster distance was observed in cluster

Table 4. Grouping of faba bean genotypes into different clusters based on D^2 analysis

Clusters	Number of genotypes	Genotypes
I	9	Vikrant, HFB-2, HFB-1, RFB-40, HPFB-20-03, HPFB-20-15, RFB-32, HPFB-20-04, RFB-45
II	5	RFB-41, HPFB-20-13, HPFB-20-16, RFB-39, RFB-42
III	16	HPFB-20-08, RFB-35, HPFB-20-02, HPFB-20-12, HPFB-20-18, HPFB-20-10, RCBMC-1, RCBMC-2, RFB-44, HPFB-20-05, HPFB-20-11, HPFB-20-14, HPFB-20-09, HPFB-20-19, HPFB-20-17, HPFB-20-01
IV	1	HPFB-20-21
V	1	HPFB-20-06
VI	1	HPFB-20-07
VII	1	HPFB-20-20
VIII	1	RFB-43

Table 5. Average intra- and inter-cluster distances

Clusters	I	II	III	IV	V	VI	VII	VIII
I	**8.22**	10.29	12.63	13.54	16.71	9.70	12.94	10.39
II		**8.42**	15.27	16.08	20.68	13.42	15.38	11.31
III			**9.64**	11.81	12.89	12.27	13.66	14.03
IV				**0.00**	9.62	14.37	11.79	14.33
V					**0.00**	14.41	13.71	18.23
VI						**0.00**	8.55	10.94
VII							**0.00**	12.43
VIII								0.00

III (9.64), followed by cluster II (8.42), signifying the presence of genetic diversity among the genotypes in that cluster. Inter-cluster distances ranged from 8.55 to 20.68. The highest inter-cluster distance in the present study was observed between clusters II and V (20.68), followed by cluster V and VIII (18.23) and cluster II and IV (16.08). Conversely, the smallest inter-cluster distance was observed between clusters VI and VIII (8.55). The large inter-cluster distances specify that the grouping of genotypes in different clusters holds broad-spectrum genetic variability. Such genetically diverse genotypes offer considerable potential for use in faba bean improvement through hybridisation programmes. Crosses involving genotypes from clusters separated by greater inter-cluster distances are expected to maximise heterogeneity and increase the probability of obtaining superior recombinants in subsequent segregating generations. Singh *et al.*[31] also reported similar findings.

Cluster Means

The cluster mean values (Table 6) revealed that cluster V showed the desired minimum values for days to flowering (85) and days to maturity (154.33). In addition, cluster V had the maximum cluster means for pods per plant (28.33), seeds per pod (3.00), biological yield (63.01g), harvest index (42.13%) and seed yield (26.53g). In addition, cluster IV showed maximum values for branches per plant (2.40), pods per node (3.49) and seeds per pod (3.00). Cluster VII exhibited

Table 6. Cluster means of eight clusters for agro-morphological and quality traits in faba bean genotypes

Traits	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V	Cluster VI	Cluster VII	Cluster VIII	Mean	Min. Value	Max. Value
DTF	94.56	95.60	89.35	87.67	85.00**	97.00*	94.67	97.00*	92.61	85.00	97.00
DTM	164.22	166.07*	161.67	161.67	154.33**	162.67	162.33	164.33	162.16	154.33	166.07
PH	48.52	48.08	46.90	56.65*	48.13	45.97**	49.51	53.97	49.72	45.97	56.65
NBP	2.05	2.21	2.10	2.40*	1.93	2.13	2.33	1.60**	2.09	1.60	2.40
NFI	2.72	2.60	2.66	2.74	2.43	2.40**	3.10	3.68*	2.79	2.40	3.68
PL	4.43	3.60**	4.70	4.77	4.96	4.23	3.95	5.17*	4.48	3.60	5.17
PW	0.97**	1.13	1.09	1.02	1.35	1.58	1.59*	1.51	1.28	0.97	1.59
NPN	2.40	2.59	2.53	3.49*	2.42	2.08**	3.14	2.35	2.63	2.08	3.49
NPP	23.06	21.96	24.38	27.00	28.33*	22.67	23.00	20.73**	23.89	20.73	28.33
NSP	2.96	2.75	2.97	3.00*	3.00*	2.87	2.20**	2.40	2.77	2.20	3.00
BY	45.55	47.33	48.18	61.25	63.01*	41.22**	49.87	45.25	50.21	41.22	63.01
HI	35.05	31.40	39.19	38.60	42.13*	38.80	32.97	31.23**	36.17	31.23	42.13
HSW	32.11	31.12**	42.65*	38.17	41.50	35.60	38.48	32.62	36.53	31.12	42.65
PC	21.48	17.86**	18.64	18.32	21.65	25.44	25.73*	19.68	21.10	17.86	25.73
SY	15.89	14.82	18.65	23.62	26.53*	15.99	16.36	14.08**	18.24	14.08	26.53

**Minimum value, *Maximum value

maximum values for pod width (1.59cm) and protein content (25.73%). Cluster VIII displayed maximum values for the number of flowers per inflorescence (3.68) and pod length (5.17 cm). Thus, choosing the genotypes belonging to these clusters for crossing programs would prove beneficial for the improvement of specific characters. Similar results were obtained by Boparai and Katna[32], Yadav *et al.*[33] and Paudel *et al*[34].

Relative Contribution of Characters Towards Divergence

The relative contribution of recorded characters towards divergence (Table 7) showed that 100-seed weight contributed the maximum (37.98%), followed by protein content (18.66 %), pod length (7.56%), pod width (6.98%), days to 50 % flowering (6.55%), biological yield per plant (5.71%) and harvest index (5.04%). Thus, these traits can be effectively utilised for the selection of parents to generate variability in the population.

Table 7. Relative contribution of different traits towards the genetic divergence among faba bean genotypes

Traits	No. of times ranked first	Contribution (%)
Days to 50% flowering	39	6.55
Days to 80 % maturity	0	0.00
Plant height (cm)	10	1.68
Number of branches per plant	5	0.84
Number of flowers per inflorescence	6	1.01
Pod length (cm)	45	7.56
Pod width (cm)	41	6.89
Number of pods per node	28	4.71
Number of pods per plant	0	0.00
Number of seeds per pod	16	2.69
Biological yield per plant (g)	34	5.71
Harvest index (%)	30	5.04
100 Seed weight (g)	226	37.98
Protein content (%)	111	18.66
Seed yield per plant (g)	4	0.67

CONCLUSION

The present investigation revealed the existence of substantial genetic variability among the faba bean genotypes for all the traits studied, indicating scope for selection and genetic improvement. High heritability coupled with moderate genetic advance for traits such as 100-seed weight and protein content indicated the predominance of additive gene action, suggesting the worth of these traits during the selection process of faba bean breeding programmes. Correlation and path coefficient analyses showed that biological yield per plant, harvest index, pods per plant, pod length, seeds per pod, 100-seed weight, pods per node and branches per plant had an impact on seed yield. The strong negative correlation of seed yield with days to 50% flowering and days to 80% maturity demonstrated the yield advantage of early-maturing genotypes. D^2 analysis suggested that the genotypes RFB-41, HPFB-20-13, HPFB-20-16, RFB-39, RFB-42 and HPFB-20-06 had considerable potential for exploiting heterotic effects through hybridisation for improving seed yield in faba bean.

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AUTHORS CONTRIBUTION

RT: Conducted the experiment, data recording and analysis PA: Wrote the original manuscript; GK: Planned the research programme, methodology, provided resources, reviewed and edited the manuscript.