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The Genetic Control of Morphological and Yield Characters in *Vicia faba* L.

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Summary. Complete diallel crosses were made within each of three populations of *Vicia faba* to examine the genetic control of morphological and yield characters. The Afghanistan and USSR populations consisted of five and the European of four genotypes. The phenotypic range of the genotypes in each population was similar for the characters studied.

In each character additive gene effects were partly responsible for genetic variation but non-additive effects varied greatly in importance depending on the population examined. Differences were found in: a) the presence or absence of dominance; b) the partitioning of the dominant effects; c) the degree and direction of dominance; d) the presence or absence of epistasis; and e) the size of narrow-sense heritability estimates.

It appears that in *V. faba* there exists much greater genetic variability than is evident by the examination of plant phenotypes. As different breeding techniques can be used to exploit different components of genetic variability, it is recommended that the possibility of differences in genetic architecture between geographical populations be taken into account in the planning of plant breeding programs. Advantage could then be taken of interactions between breeding methods and populations that are phenotypically but not genetically similar.

Key words: Field bean – Faba bean – Diallel analysis – Plant breeding

Introduction

The field or broad bean (*Vicia faba* L.) has been cultivated for thousands of years in many parts of the world (Renfrew 1973; DeCandolle 1886). Yet despite this long history of cultivation, yields are nowadays often uncompetitive and highly variable, especially under intensive agriculture in developed countries. Breeding programs to improve the potential of the crop are continuing in many localities (eg. at the Plant Breeding Institute, England, and the Welsh Plant Breeding Station, Wales), but progress is slow. One possible reason for this limited advance is that *V. faba* appears to exhibit little phenotypic variation and has been presumed to be a species with a narrow genetic base.

Clausen and Hiesey (1958) have summarized and discussed much of the available evidence that shows that phenotypic and genotypic differences exist between geographically separable populations within a species. Most studies of this type, however, have demonstrated major gene differences between phenotypically distinct populations within a wild species. Differences in quantitative inheritance have rarely been described within a species where phenotypic expression is similar. However, when the techniques for the study of quantitative variation have been applied to the study of different populations within a species, whether wild (e.g. *Papaver dubium* L.; Lawrence 1965) or cultivated (e.g. *Pisum sativum* L.; Snoad and Arthur 1973), such differences of genetic control were found.

It was considered possible, therefore, that more complex variation exists in *V. faba* than is evident at the phenotypic level. In this paper the genetic control of twelve traits is characterized in three phenotypically similar populations from different geographical areas using the Jinks (1954) and Hayman (1954a, b) diallel analysis. Characters are studied which might well have been affected by human selection (yield characters) and those which would not necessarily have been so affected (morphological characters). Population differences in the mode of inheritance of each character are examined and the implications to plant breeding of the phenotypic masking of genetic variability are discussed.

Materials and Methods

The populations studied consisted of five genotypes from Afghanistan, Group A, (PI's 222129, 223303, 223418, 254006 and

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317500), five from the USSR, Group U, (PI's 319896, 319898, 319900, 319901, 319902) and four from Europe, Group E, (cultivars 'Compacta', 'Longpod', 'Maris Bead' and 6075, a field bean selected for small stature from 'Ackerperle'). The genotypes within each of the three populations were crossed in all possible combinations in the winter of 1976, producting three separate, complete diallels. Groups A and U each had twenty-five families while group E contained sixteen. The F_1 and selfed plants were grown in a bee-proof greenhouse during the summer and each plant was self-pollinated by hand. The F_2 was then planted in the filed at the Oxford University Field Station in the spring of 1977 in a randomised complete-block design with six replications. The plants were spaced at 15 cm within rows with 50 cm between rows and each family was grown together in a row within each plot. In most cases seven plants per family per block developed but in some instances fewer plants were measurable due to poor seed set in the F_1 or bad germination in the field. Within-block family means were therefore used as raw data.

The following morphological characters were scored:

a) Number of days from germination to flowering (DTF);
b) Height (HT);
c) Number of podded tillers per plant (NOPT);
d) Mean number of flowers at the second, third and fourth inflorescence on the main stem – an estimate of number of flowers per node (FL/N);
e) Number of flowering nodes on the mainstem (NOFN).

The following yield characters were scored:

a) Number of seeds per pod (SD/PD);
b) Number of pods per podded node (P/PN);
c) 100 seed weight (SDWT);
d) Number of seeds per plant (SD/PL);
e) Number of podded nodes (NOPN);
f) Number of pods per plant (P/PL);
g) Seed weight per plant (YIELD).

FL/N and NOFN were scored on only three of the six blocks.

Data were analysed by the diallel method of Hayman (1954a, b) and Jinks (1954) as summarized by Mather and Jinks (1971). Jinks (1956) describes the modifications required to estimate components of variation from F_2 data. The method of diallel analysis makes certain assumptions concerning the genetic system investigated and each of these were tested for the data presented. These assumptions are:

i) Diploid inheritance. *V. faba* segregates in a diploid manner.

ii) Homozygosity of parental lines. *V. faba* is a partial outbreeder (Soper 1952; Rowlands 1958; Bond 1976) so it is possible that the genotypes were not totally homozygous. However, inbreeding of lines had been undertaken and it was likely that only slight residual heterozygosity remained. Most importantly, the differences between parents were very much greater than those within parental types. The triangulation of the Wr/Vr graph, an indication of residual heterozygosity in the parents (Dickinson and Jinks 1956), was not evident in any character in any population.

iii) No reciprocal differences between crosses. When these occurred their effects were removed by replacing entries in the diallel table with the mean of the reciprocal crosses.

iv) Independent action of non-allelic genes. This was tested for by examining the regression between the array variances (V_r) and the parent-offspring covariances (W_r) and by examining the analysis of variance of $W_r - V_r$ values for each character. When a simple additive-dominant model is adequate the W_r/V_r regression is expected to differ significantly from 0 but not from 1 and $W_r - V_r$ is expected to be constant over arrays. Where this assumption is not met large errors in the estimates of components of variation may be produced. These estimates will be reported in this paper for completeness, but not discussed in detail.

v) Multiple allelism does not exist. Presence of this would be detected by heterogeneity of the $W_r - V_r$ values over arrays and by the W_r/V_r regression differing significantly from 1.

vi) No genotype × environment interactions. This was tested for by the method of Mather and Jinks (1971).

In the Hayman (1954a) analysis of variance the partitioning of the variances primarily tests the significance of the following effects:

a = the additive effect of the genes;
b = the dominance effects of the genes;
b_1 = directional dominance;
b_2 = assymetry of the distribution of dominant genes in the parents;
b_3 = dominance interaction between specific genotypes (same as the specific combining ability of Griffing 1956);
c = reciprocal effects due to maternal effects;
d = reciprocal effects other than maternal ones;
B = blocks.

The error variance used was the Blocks total (BT) as Bartlett's tests showed that heterogeneity of block interaction variances was negligeable. However, in those instances where the c mean square was significant it became the correct error mean square for testing the a item, and where the d mean square was significant it similarly became the correct error mean square for testing the c and b items (Wearden 1964). The correlation between $W_r + V_r$ and parental means indicated the direction of dominance for a character within a population. A negative correlation coefficient approaching –1 indicated that dominant alleles acted to increase the expression of the character, a positive value approaching +1 indicated that recessive alleles increased the expression and a value approximating to 0 indicated ambidirectional dominance. Additive (D) and dominance (H_1 and H_2) components were estimated. F was an indication of the relative frequency of dominant and recessive alleles in the parental population and was positive when an excess of dominant alleles was present and negative when recessive alleles were in excess. The measure of the degree of dominance $(H_1/D)^{1/2}$ was less than 1 for partial dominance, equal to 1 for total dominance and greater than 1 for overdominance. Narrow sense heritability (NSH) was calculated by the method of Mather & Jinks (1971).

Results

Morphological Characters

DTF – Dominance due to directional and specific interaction effects was significant in E but reciprocal effects were present in the other two populations (Table 1) and dominant effects could not be tested with the same precision. No epistasis was evident (Table 2) and further analysis showed the direction of dominance decreased flowering time in A and E but was ambidirectional in U. Recessive alleles were in excess in E but not in A or U and the degree of dominance was par-

Table 1. Mean squares of genetic components for morphological characters

Item	DF	DTF	HT	NOPT	DF	FL/N	NOFN
Afghanistan (A)							
a	4	233.2**	1,079.8**	1.40**	4	2.60**	47.33**
b	10	14.3	75.4*	0.41**	10	0.32	2.48**
b_1	1	29.9	126.3	2.08**	1	0.46	0.44
b_2	4	44.0	36.2	0.31**	4	0.53*	0.16
b_3	5	19.2	96.6*	0.15	5	0.12	4.74**
c	4	13.7	30.7	0.19	4	0.01	4.48**
d	6	5.4*	27.4	0.12	6	0.09	0.83
B	5	26.1**	2,247.2**	2.04**	2	0.13	0.59
BT	120	1.9	37.8	0.08	48	0.16	0.77
USSR (U)							
a	4	196.2**	1,535.3**	1.00**	4	7.00**	56.87**
b	10	11.9	88.5*	0.21*	10	0.95**	0.82
b_1	1	4.8	410.3**	1.14*	1	2.34**	1.44
b_2	4	4.4	35.8	0.12	4	0.92**	0.53
b_3	5	19.2	66.2	0.09	5	0.72**	0.73
c	4	7.6	38.4	0.12	4	0.79**	2.67
d	6	21.3**	28.3	0.08	6	0.39	0.81
B	5	17.3*	1,539.4**	2.07**	2	0.20	0.56
BT	120	6.4	38.5	0.09	48	0.19	1.12
Europe (E)							
a	3	1,224.2**	6,174.8**	0.78**	3	9.45**	34.00**
b	6	50.8**	436.9**	0.53**	6	1.43**	5.09**
b_1	1	65.9**	1,297.5**	1.71**	1	4.66**	14.57**
b_2	3	4.9	373.1**	0.07	3	0.59	2.54*
b_3	2	112.0**	102.3	0.65**	2	1.07	4.18*
c	3	10.6	14.1	0.07	3	0.28	0.02
d	3	7.8	148.7	0.02	3	0.33	1.25
B	5	25.5**	1,392.4**	1.13**	2	0.55	0.71
BT	75	4.7	86.4	0.08	30	0.33	0.87

* Significance at the 5% level
** Significance at the 1% level

tial in U but total in A. Narrow sense heritability varied between populations from 38 to 73%.

Ht – Dominance was significant in all populations (Table 1) but was of a directional type in E and U and due to specific genotype combinations in A. Epistasis was not evident (Table 2) and while dominant alleles increased height in U and E they acted ambidirectionally in A. There was an excess of negative alleles in A but an excess of positive alleles in the other populations. The estimates of degree of dominance varied from partial dominance in E, to total in A, to overdominance in U. Despite these genetic differences, narrow sense heritability was similar in all populations at 40–46%.

NOPT – Dominance effects were important in all populations (Table 1) but, while directional dominance was significant in all three, interactions between specific genotypes were important only in E. Epistasis was evident in A and E while in U the additive-dominance model just fitted the data (Table 2). Populations showed an increase in the number of podded tillers associated with dominant alleles, and excess of dominant alleles in A and U and of recessive in E, overdominance and low heritability.

FL/N – Dominance effects varied from population to population, with little evidence of dominance significant in A, directional dominance significant in E and all forms significant in U (Table 1). U also showed maternal reciprocal effects. No epistasis was evident in any population (Table 2). Dominant alleles increased the character in A and E but has an ambidirectional effect in U. Overdominance was evident in all populations while heritability varied from 27% in E to 55% in U.

NOFN – While dominance was present due to specific interactions in A and all dominance items were significant in E, only additive effects were demonstrable in U (Table 1). A also exhibited maternal reciprocal ef-

Table 2. Morphological characters – summary of Wr/VR graph results and components of variation

Character	Population	Wr/Vr slope	Wr – Vr	$r\bar{p}$. Wr + Vr	D	H_1	H_2	F	$(H_1/D)^{1/2}$	NSH
DTF	A	0.88 ± 0.09	ns	+0.93	16.70	17.72	16.80	2.99	1.04	54.4
	U	1.18 ± 0.14	ns	+0.27	14.29	6.53	7.64	2.89	0.68	38.1
	E	0.94 ± 0.02	ns	+0.99	90.13	61.61	61.88	−22.97	0.83	73.7
HT	A	0.89 ± 0.11	ns	−0.13	49.90	49.54	52.17	−39.47	1.00	46.0
	U	0.94 ± 0.14	ns	−0.84	120.62	65.93	68.88	41.26	1.60	40.7
	E	0.95 ± 0.08	ns	−0.91	776.40	762.39	474.36	585.87	0.85	40.4
NOPT	A	0.74 ± 0.23	*	−0.89	0.11	0.52	0.44	0.09	2.20	22.0
	U	0.75 ± 0.23	ns	−0.94	0.09	0.18	0.17	0.06	1.46	12.9
	E	0.83 ± 0.32[a]	ns	−0.79	0.04	0.59	0.16	−0.04	3.81	12.3
FL/N	A	0.85 ± 0.16	ns	−0.88	0.10	0.70	0.43	−0.31	2.68	55.8
	U	1.06 ± 0.29	ns	−0.23	1.06	2.63	2.06	0.61	1.58	42.2
	E	0.92 ± 0.14	ns	−0.83	2.25	3.11	2.99	1.55	1.18	27.6
NOFN	A	1.03 ± 0.24	ns	−0.58	5.82	4.07	4.64	1.02	0.84	61.9
	U	1.08 ± 0.12	ns	−0.69	8.31	−1.28	−0.68	1.51	–	–
	E	1.00 ± 0.11	ns	−0.98	7.69	12.38	11.41	4.94	1.27	33.5

[a] Slope not significantly different from 0; ns = heterogeneity over arrays not significant at 5% level
* Heterogeneity over arrays significant at 5% level

fects. No epistasis was evident in any population (Table 2) and dominant alleles, when present, tended to increase the number of flowering nodes. The negative values of the components of analysis for U, theoretically impossible in second order statistics, were taken as being estimates of zero, again showing that little dominance was present in this population. The A and E population differed slightly in their degree of dominance and greatly (62% for A and 34% for E) in their heritability.

Yield Characters

SD/PD – Directional dominance was evident in E while non-maternal reciprocal effects were present in both A and U (Table 3). Non-allelic interaction was indicated in E but not in A or U (Table 4). Despite these similarities between A and U, dominant alleles have opposite expressions in the two populations and while dominance was partial in A overdominance was present in U. Heritability was estimated at 66.6% in A but only 10.7% in U.

P/PN – Dominance was present in A due to specific interactions and in E due to all factors, but was not significant in U where reciprocal differences were evident (Table 3). Epistasis was not indicated in any population (Table 4) and dominant alleles decreased pods per podded node in A and E yet had ambidirectional effects in U. Slight differences between populations were indicated in the degree of dominance, and heritability ranged from 30–57%.

SDWT – The significance of dominance effects varied between populations (Table 3). Specific interactions are significant in U, all effects are signficant in E but there is no indication of dominance in A, where reciprocal differences were present. Epistasis is evident in U (Table 4) but not in A or E. While dominant alleles had differing effects in the A and E populations both showed an excess of recessive alleles, a tendency to partial dominance and high heritability.

SD/PL – Directional dominance was present in all populations (Table 3) but epistasis was also demonstrated in A (Table 4). The U and E populations differed in the effect of dominant alleles, the degree of dominance and the estimate of heritability.

NOPN – Directional dominance was significant in all populations but dominance due to specific interaction was also significant in E (Table 3). Epistasis was evident in all populations (Table 4) but dominant alleles tended to increase the number of podded nodes in each and all displayed evidence of overdominance and a heritability of about 35%.

P/PL – Dominance was significant in all populations (Table 3), due to directional effects in both A and E and due to specific effects in A. Epistasis was evident in A (Table 4). In E and U dominant alleles were ambidirectional, partial to total dominance was evident in E with overdominance in U and heritability estimates were 45% for U and 68% for E.

YIELD – All populations showed directional dominance (Table 3) but epistasis was present in both A and U (Table 4). Overdominance was evident in E and heritability was very low.

Discussion

The inheritance of twelve characters have been studied here in diallel experiments involving genotypes from three geographically separate populations. The use of

Table 3. Mean squares of genetic components for yield characters

Item	DF	SD/PD	P/PN	SDWT	SD/PL	NOPN	P/PL	Yield
Afghanistan (A)								
a	4	3.38**	1.16**	2,257.8**	755.0**	109.1**	116.3**	306.7*
b	10	0.10	0.08**	25.0	339.8*	18.0**	74.0**	88.4**
b_1	4	0.02	0.01	36.2	2,216.9**	104.4**	393.2**	584.1**
b_2	4	0.06	0.03	15.2	158.3	8.5	35.2	62.9*
b_3	5	0.16	0.14**	30.6	109.3	8.3	41.2*	9.6
c	4	0.08	0.03	13.6	325.4	6.6	31.6	47.4
d	6	0.14**	0.05	42.6**	127.4	15.0	26.9	4.3
b	5	0.61**	0.31**	11.7	2,888.8**	52.4**	209.3**	502.6**
BT	120	0.04	0.03	5.3	144.9	3.8	16.0	19.9
USSR (U)								
a	4	0.49**	0.71**	3,987.1**	4,217.8**	46.4**	417.8**	894.2**
b	10	0.29	0.09	206.0**	507.8**	10.8**	55.4**	154.4**
b_1	1	0.47	0.09	3.3	2,628.0*	56.6**	235.1**	418.8**
b_2	4	0.47	0.13	265.9**	432.3	12.1**	70.2**	250.1**
b_3	5	0.10	0.06	198.5**	144.1	0.7	7.7	25.0
c	4	0.14	0.06	22.2	21.2	1.8	15.8	5.9
d	6	0.15*	0.12**	17.4	181.8	4.5	19.5	46.6
B	5	0.31**	0.30**	163.2**	2,763.0**	67.8**	204.5**	844.5**
BT	120	0.06	0.04	13.1	178.7	3.2	16.6	40.1
Europe (E)								
a	3	2.68**	6.55**	33,151.3**	10,537.8**	73.2**	1,100.6**	149.5*
b	6	0.67**	0.57**	600.5**	475.0*	15.7**	48.5**	295.2**
b_1	1	1.48**	0.36*	283.2*	1,301.1*	38.9**	5.3	1,060.2**
b_2	3	0.55*	0.32**	368.9**	346.5	10.0*	73.8**	231.2**
b_3	2	0.46	1.04**	1,106.7**	514.9	12.7**	32.2	8.5
c	3	0.22	0.05	55.0	12.7	0.6	0.6	18.0
d	3	0.07	0.08	26.1	45.3	2.3	4.8	18.2
B	5	0.66**	0.11*	129.3*	1,605.8**	23.6**	92.6**	632.4**
BT	75	0.19	0.04	49.4	205.3	2.5	13.7	46.1

* Significance at the 5% level
** Significance at the 1% level

the Hayman-Jinks diallel analysis, rather than the analyses of Griffing (1956) or Comstock and Robinson (1952) meant that relatively few parents could be examined per population and that the results could not necessarily be related to the overall population from which the studied plants were taken. It did, however, provide a complete analysis including tests for non-allelic interaction and thereby produced a greater amount of information for these parents than would otherwise have been obtained.

Data in Tables 1–4 may be used to identify those parents which, when crossed, are likely to produce progeny that can be selected rapidly and effectively for enhancement of a desired character. Those characters most likely to respond to selection can also be recognized (e.g. NSH of SDWT was generally high while that of YIELD or NOPT was generally low). Such genetic information may, therefore, be used to augment the success of the largely empirical techniques of the plant breeder. This data also showed, however, that the partitioning of the genetic variance of any character depended on the population of plants examined and varied greatly from one plant group to another. Although the data presented were only from three populations in one environment, differences in the methods of control of most of the characters existed within the species even when examining similar phenotypes. Differences between populations were found in: a) the presence or absence of dominance; b) the partitioning of the b (dominance) items in the Hayman's analysis; c) the degree and direction of dominance; d) the presence or absence of epistasis; and e) the size of narrow-sense heritability estimates.

Other published data also indicates that the overall estimates of genetic components alter as the population under study changes. For example, results for *V. faba* shown here for group E are comparable to the results of Bond (1966) where a

Table 4. Yield characters – summary of Wr/Vr graph results and components of variation

Character	Population	Vr/Wr slope	Wr – Vr	$r\bar{p}$. Wr + Vr	D	H_1	H_2	F	$(H_1/D)^{½}$	NSH
SD/PD	A	0.93±0.13	ns	+0.77	0.20	0.09	0.09	0.04	0.67	66.6
	U	0.90±0.20	ns	−0.94	0.10	0.46	0.30	0.23	2.13	10.7
	E	0.78±0.26[a]	ns	−0.84	0.10	0.78	0.67	−0.16	2.84	34.1
P/PN	A	1.18±0.15	ns	+0.71	0.09	0.06	0.07	0.03	0.84	36.6
	U	1.48±0.22	ns	−0.36	0.05	0.10	0.07	0.04	1.38	30.9
	E	0.99±0.14	ns	+0.97	0.55	0.80	0.70	0.05	1.21	57.2
SDWT	A	0.95±0.03	ns	−0.60	126.20	30.33	26.63	−46.02	0.49	88.0
	U	0.85±0.11	**	+0.91	308.01	358.33	257.86	136.73	1.08	63.6
	E	0.95±0.06	ns	+0.99	2,721.97	841.41	738.97	−19.79	0.56	85.9
SD/PL	A	0.35±0.14[a]	ns	−0.97	66.21	265.84	267.87	53.90	2.00	0.2
	U	0.92±0.26	ns	−0.67	200.24	540.42	448.42	−87.30	1.64	39.5
	E	1.05±0.09	ns	+0.48	845.99	318.13	282.16	−3.58	0.61	61.6
NOPN	A	0.68±0.26[a]	*	−0.65	3.97	20.78	19.11	−5.16	2.29	38.5
	U	0.69±0.28[a]	ns	−0.90	2.46	13.83	10.42	0.93	2.37	30.0
	E	0.84±0.27[a]	ns	−0.81	6.48	20.16	17.86	2.43	1.76	31.4
P/PL	A	0.25±0.30[a]	ns	−0.63	1.48	85.03	78.21	−6.53	7.57	17.3
	U	0.93±0.29	ns	−0.46	14.49	73.22	52.69	−13.80	2.25	45.1
	E	1.01±0.13	ns	+0.46	82.33	66.55	47.63	−6.46	0.90	67.8
Yield	A	0.40±0.42[a]	ns	−0.46	1.81	108.53	92.38	−26.01	7.74	33.8
	U	1.69±0.04[b]	ns	+0.92	126.15	236.41	154.56	180.42	1.37	14.9
	E	0.88±0.05	ns	−0.93	37.26	393.74	335.90	88.14	3.25	0.0

[a] Slope not significantly different from 0; [b] Slope significantly different from 1; ns = heterogeneity over arrays not significant at 5% level

* Heterogeneity over arrays significant at 5% level

** Heterogeneity over arrays significant at 1% level

European population was studied, yet differ markedly from the results of Carter (1975) where a population consisting of Russian, Sudanese and European types was examined. Riggs and Hayter (1972, 1973) also showed differences in genetic parameters between two- and six-rowed barley and it is probable that other crops demonstrate such genetic variation between populations where natural or induced genetic barriers have reduced interbreeding.

It follows that, where the genetic basis of the character varies between populations, the breeder may alter the expression of genetic parameters in experimental material by the careful selection of parents. Populations consisting of plants from widely separate origins may give very different results to those consisting of plants all from the same geographical area and the effectiveness of selection would be correspondingly altered. Breese (1972) states that the way in which a polygenic, economic character is inherited (via additivity, dominance or epistasis) can determine breeding methods and that strategy and tactics in plant breeding depend on the knowledge of the genetic and environmental components of variation. Therefore, different breeding techniques can be used to exploit different components of variation. Inbred varieties exploit additive effects and non-allelic interaction between homozygotes; hybrid varieties exploit dominance and non-allelic interaction between heterozygotes; open-pollinated varieties can exploit additive or dominance effects and all types of non- allelic interaction, depending on the method of selection employed. As the breeding system in *V. faba* ranges between in- and outbreeding, and as data presented here indicates that for most characters genetic control varies between populations, it may be deduced from Breese (1972) that virtually all breeding methods could be used in the construction of varieties in this species. Thus a breeder may be able either to select the population which displays the method of inheritance of a character to suit his breeding program, or to choose his program to suit his population. The relatively small success of the great variety of breeding methods being employed to improve *V. faba* may be indicative of this need to match population to method.

Since all genotypes of *V. faba* available today are cultivars, no wild types being known, the crop is entirely under the influence of man. It might be argued that during cultivation selection would have been made for yield characters rather than for possibly unimportant morphological ones. Therefore, since the former would be characters affecting fitness, they should display the genetic properties described by Mather (1966), namely: a) little heritability; b) non-allelic interaction, usually of

the duplicate type; and c) dominance in the direction of selection. In the data presented here there is evidence that yield characters are determined by epistasis more often than morphological ones – nine out of twenty-one analyses display evidence of epistasis in the former and two out of fifteen in the latter, both of these being in a character that might be associated with yield (NOPT). However, there ist little evidence that yield characters express less heritability or a greater expression of directional dominance than do morphological characters and so the expected fitness characters do not exhibit the expected fitness genetics. In addition, if past selection for yield characters had been rigorous then all populations might be expected to display the same modes of inheritance. Tables 3 and 4 show that this is not the case. This suggests, therefore, either that the yield characters have not been selected for with any success, or that increased yield has been selected for in different ways in different populations. This indicates that all the potential genetic variation within the genepool of *V. faba* has not been fully exploited for breeding purposes. If a character has been judged unimportant in one area yet important in another, the genetic architecture of the two populations may well differ. The deliberate introduction of specimens from the former area to the latter might, therefore, also introduce a genetic architectural system that would be much more susceptible to directional selection under the new conditions. Therefore, such introductions might produce rapid, immediate improvement in that feature.

This paper has attempted to examine the wide genetic variation that is present even in species with as narrow a phenotypically expressed genetic base as *V. faba*. Characterization of this variation provides the plant breeder with information on the genetic diversity of the crop, the probability of success in selecting a desirable character and the best methods and genotypes to use for that selection. In *V. faba* the identification and use of wider genetic variability may increase and stabilise yield and hence make it a more agriculturally competitive crop.

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