FERTILITY STUDIES IN THE FIELD BEAN (*VICIA FAB*A L.)

II. INBREEDING

D. G. ROWLANDS

Welsh Plant Breeding Station, Aberystwyth *

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1. INTRODUCTION

PREVIOUS work has indicated that *Vicia faba* is a naturally cross-pollinating species but under field conditions insect pollination appears to be inadequate and much of the seed that is set (up to 70 per cent. of the total) results from self-pollination (Rowlands, 1958, 1960). Moreover, the average proportion of flowers that set in the field is 20-25 per cent., which suggests that even self-pollination is not very successful, in fact data from controlled self-pollination indicate considerable self-sterility.

A hypothesis was put forward in the first paper to explain this self-sterility in terms of homozygosity of deleterious recessive genes which can accumulate in any outbreeding system.

Breakdown of the original outbreeding system resulting from migration of the species from its centre of origin and cultivation practices, coupled with unsatisfactory insect pollination, could be followed by zygotic sterility caused by deleterious recessive genes. The present system is, therefore, one of balance where the pressure to inbreed is counteracted by the requirement for "tripping" of the flowers and zygotic infertility.

From the point of view of yield improvement it would appear that reliance on insect pollination for seed production introduces too much uncertainty, but in common with other cross-fertilising plants, inbreeding in beans results in loss of vigour. Nevertheless for ease of handling, a self-tripping, self-fertile, line would offer great advantages. Inbreeding in field beans is therefore here discussed in relation to the use of pure lines in improvement work.

2. PRELIMINARY STUDIES

The use of a white-flowered line (Ch 170) of field beans enabled a comparison of hybrids and inbreds to be made. Alternate rows of the white-flowered (recessive) and coloured-flowered (dominant) lines were grown and the progeny from the white-flowered line separated into outcrossed or inbred types in the subsequent year. (The white-flowered line originated from a single plant and was already inbred.) The distribution of flower number and pod number per plant in the two groups of material under field conditions is shown in fig. 1.

* Now at Unilever Research Laboratory, Colworth House, Bedford.

In the case of both flowers and pods, a wide variation characterises the outcrosses while this variation is much reduced in the inbreds. Moreover, mean flower and pod number is lower in the inbred than in

FIG. 1.—Frequency distribution of flowers and pods per plant in inbred and outcrossed bean plants.

the crossbred material. Some of the inbred material did, however, produce more than 20 pods per plant and this suggested further investigation into the behaviour of pod setting during inbreeding.

3. GENERAL INBREEDING STUDIES IN THE GLASSHOUSE

Material was selected for study from six field populations namely:

- Ch 170 the white-flowered already inbred line
- Ch 4 a commercial stock of tick beans
- B 26 a selection from Ch 4
- Ch 103/2 a selection from a commercial line (*ex* Dorset)
- Ch 35/2 a selection from a commercial line (*ex* Devon)
- Cp 145 a high-yielding flower colour selection.

Two samples of five plants were taken from each of the populations, one comprising five very good podding plants, and the other, five plants taken at random. In the case of Ch 170 five additional good plants were taken (A selections) and from the Ch 4 population five of the worst podding plants that could be found. The pod numbers of each of these parent plants are shown in table 1.

TABLE 1

Pod numbers of parent plants for inbreeding experiment (open-pollination, 1955)

Population		Plant reference no.					Mean
		1	2	3	4	5	
Ch 170	Selected . . .	78	70	79	64	117	81.6
	A Selection . . .	55	50	48	51	61	53.0
	Random * . . .	...	...	...	...	...	...
Ch 4	Selected . . .	40	39	35	35	32	36.2
	Random . . .	31	24	24	15	21	23.0
	Worst . . .	11	13	11	11	14	12.0
B 26	Selected . . .	29	44	36	33	70	42.4
	Random . . .	13	24	12	9	30	17.6
Ch 103/2	Selected . . .	37	29	43	56	40	41.0
	Random . . .	33	9	14	23	8	17.4
Ch 35/2	Selected . . .	27	31	38	28	43	33.4
	Random . . .	26	23	10	15	11	17.0
Cp 145	Selected . . .	29	42	28	45	42	37.2
	Random * . . .	...	...	...	...	...	...

* Pod numbers were not recorded for random plants of Ch 170 and Cp 145.

Five progeny plants from each original parent were grown in an insect-proof glasshouse during 1956 and pod and seed number per plant recorded on each individual. As many flowers as possible were artificially manipulated to simulate the effect of tripping, so that the data obtained reflected the capacity of each plant to set selfed seed.

The most significant point in table 2 is the low pod-setting on selfing as compared with the performance of the parental lines under open-pollination. This progeny performance on selfing is not correlated with the parental pod set, and their self-fertilities are all of the same order. In general, the selected material would appear to possess lower self-fertilities than the random material. This is to be expected if the selected parents are highly podding by virtue of heterozygosity for self-sterility genes, and this superiority would not be apparent in their progeny. Despite the rather low mean pod number per plant, most of the lines contained occasional plants producing 15-20 pods, which may be regarded as an adequate set in the field. Seed production

per plant, and also the mean number of seeds per pod, are reduced, selected plants again suffering more than random plants.

TABLE 2
Mean pod and seed setting of parental lines and S_0 segregates from each (1956)

		Parental pod mean (open-pollination)	Pods per plant on selfing S_0 segregates			Seeds per	
			Mean	Range	Per cent. of parent	Plant	Pod
Ch 170	Selected .	81.6	7.2	0-20	8.8	14.2	1.9
	A Selection	53.0	9.7	4-22	18.3	...	...
	Random .	...	5.6	0-28	...	12.3	2.2
Ch 103/2	Selected .	41.0	9.8	0-29	23.0	20.4	2.1
	Random .	17.4	10.2	0-26	58.6	21.6	2.1
Ch 35/2	Selected .	33.4	7.0	2-28	21.0	14.7	2.1
	Random .	17.0	10.0	4-23	58.8	20.6	2.1
B 26	Selected .	42.4	6.7	0-13	15.8	11.8	1.8
	Random .	17.6	7.7	1-15	43.8	14.9	1.9
Ch 4	Selected .	36.2	7.8	1-19	21.5	12.1	1.6
	Random .	23.0	8.1	0-20	35.2	15.1	1.9
	Worst .	12.0	6.2	1-12	51.7	14.3	2.3
Cp 145	Selected .	37.2	6.0	0-10	16.1	15.0	2.5
	Random .	...	6.6	1-21	...	15.3	2.3
Mean . . .		34.3	7.8	...	31.1	15.6	2.1

From this population, those plants bearing 20 or more pods or more seeds per plant were selected. Fifty seeds of each of the eight highest lines were sown, together with five seeds of each of seventeen fairly good lines. In addition, five seeds of each of the 22 progenies of Ch 4 were sown. These plants were allowed to set seed without the aid of "tripping" and an estimate of spontaneous self-fertility was obtained. These results are presented in table 3.

Pod number per plant is lower than the corresponding progeny mean in 1956, and very much lower than in the selected parental S_0 plants. Seed number per plant is reduced and so is the percentage of flowers setting pods, and the mean seed number per 100 flowers. Some of the progenies contain a high proportion of sterile plants; Ch 103/2 progenies in general were worse than the others, and Ch 103/2R3/2 were worst of all, with over 50 per cent. of the plants sterile. Least affected by inbreeding is Ch 170 R 5/2 with fewest sterile plants and highest pod and seed sets. The family Ch 170 is based on a single white-flowered plant and is already somewhat inbred. Ch 170 R 5/2, Ch 35/2 R 3/1 and Ch 103/2 S 2/4 are perhaps the most profitable progenies to follow up in attempting to select for self-fertility.

TABLE 3

Mean self-fertility of S₁ progenies from highly self-fertile S₀ plants (1957)

Progeny	No. of plants grown	No. of pods on S ₀ plants	Per cent. sterile plants	Mean no. per plant of			Mean no. of seeds per pod	Per cent. flowers forming pods	Seeds per 100 flowers
				Flowers	Pods	Seeds			
Ch 170 R 5/2 .	32	28	3	125	5.7	9.6	1.7	4.6	7.7
Ch 35/2R3/1 .	44	23	5	119	4.8	7.5	1.6	4.0	6.3
Ch 35/2R4/1 .	43	22	14	127	4.3	6.0	1.4	3.4	4.7
Ch 35/2S3/2 .	49	28	16	125	3.9	5.1	1.3	3.1	4.2
Ch 103/2R1/1 .	37	21	27	140	2.4	2.4	1.0	1.6	1.6
Ch 103/2R4/1 .	41	26	32	133	2.1	2.5	1.2	1.6	1.9
Ch 103/2R3/2 .	38	24	58	98	3.9	1.0	0.3	4.0	1.0
Ch 103/2S2/4 .	42	29	17	109	5.4	9.1	1.7	5.0	8.4
Mean . .	...	25.1	21.5	122	4.1	5.4	1.3	3.4	4.4

TABLE 4

Pod and seed setting in S₁ progeny plants and S₂ families of Ch 170 R 5/2 (1958)

Progeny no.	S ₁ progeny plants			S ₂ family means		
	No. of			No. of		
	Pods	Seeds	Seeds per pod	Pods	Seeds	Seeds per pod
1	3	4	1.3	12.5	21.5	1.7
2	18	35	1.9	2.4	4.2	1.8
3	1	2	2.0	2.0	3.5	1.8
4	6	9	1.5	8.0	17.0	2.1
5	2	2	1.0	4.5	8.0	1.8
6	6	11	1.8	5.0	7.8	1.6
7	2	4	2.0	6.0	11.7	2.0
8	14	17	1.2	5.0	8.0	1.6
9	10	17	1.7	9.3	19.7	2.1
11	1	1	1.0	2.7	4.3	1.6
13	9	18	2.0	9.5	16.0	1.7
14	5	5	1.0	8.0	12.7	1.6
16	6	8	1.3	0.5	0.5	1.0
17	4	8	2.0	2.3	4.0	1.7
18	7	15	2.1	3.3	6.0	1.8
20	4	7	1.8	6.5	16.0	2.5
21	16	27	1.7	10.0	17.0	1.7
22	9	15	1.7	3.3	6.8	2.1
23	5	11	2.2	3.0	6.3	2.1
24	3	8	2.7	17.0	34.0	2.0
25	7	10	1.4	15.0	32.0	2.1
26	3	1	0.3	9.0	10.0	1.1
27	3	3	1.0	2.0	3.5	1.8
28	4	10	2.5	5.4	10.6	2.0
29	1	2	2.0	18.0	38.0	2.1
30	5	6	1.2	11.5	18.0	1.6
31	11	19	1.7	7.3	11.0	1.5
32	2	5	2.5	6.3	14.3	2.3
Mean .	5.9	10.0	1.7	5.9	11.0	1.8

In contrast to the above material the less highly fertile S_0 progenies were only scored for pod and seed number but the data were comparable with those obtained from the more highly fertile S_0 plants.

Progenies from Ch 103/2 were again generally of lower self-fertility, while Cp 145 S 2/3 was highest in this group, but taken as a whole the group showed no lower pod and seed set than the progenies from highly fertile S_0 plants.

Line Ch 170 R 5/2 was continued in its entirety in 1958, five segregates representing each of the S_1 progeny from the previous year. Of

TABLE 5
Pod and seed setting in S_3 progenies of Ch 170 R 5/2

Progeny no.	S ₃ progeny			No. of plants per S ₃ progeny
	Mean no. of			
	Pods	Seeds	Seeds per pod	
1/2	3.1	5.4	1.7	15
4/1	4.1	7.5	1.8	14
7/2	2.2	3.4	1.5	12
9/1	6.4	11.6	1.8	15
9/2	9.7	18.6	1.9	12
13/1	1.4	2.4	1.7	3
20/1	4.7	10.5	2.2	15
21/22	11.4	23.5	2.1	11
21/1D	11.6	28.2	2.4	10
10/1D	6.0	12.4	2.1	8
24/1	2.5	4.8	1.9	15
25/1	5.4	9.9	1.8	13
29/1	5.6	10.0	1.8	15
	5.7	11.4	1.9	...

the other lines, five plant progenies were sown of Ch 35/2 R 3/1 and Ch 103 S 2/4 and, in addition, five plant progenies (where seed permitted) of the highly self-sterile line Ch 103/2 R 3/2. Pod and seed number per plant were again recorded and the data for Ch 170 R 5/2 are given in table 4.

Pod and seed number per plant are slightly improved in 1958 although no conscious selection has been practised for this factor. If, however, the 1958 population had been based only on those plants with 16 or more seeds, the means for pods and seeds would be 7.3 and 12.6 (compared with 5.9 and 11.0 for unselected plants). In this family, selection would have improved self-fertility. In Ch 35/2 R 3/1 and Ch 103/2 S 2/4 where some selection was in fact practised the means were maintained in the former (4.1 for pods and 7.3 for seeds) while they fell in Ch 103/2 S 2/4 (to 3.0 for pods and 6.0 for seeds). The low fertility line Ch 103/2 R 3/2 had a lower pod set (0.97 per

plant) but maintained seed setting at 1.6 per plant, with again over 50 per cent. self-sterile plants.

The 1959 material was based on progenies from S_2 plants which bore over 20 seeds. S_3 progeny means for pods and seeds per plant and seeds per pod are given in table 5.

TABLE 6

Pod and seed setting in parent plants, S_0 plants and S_1 progenies of Ch 4

Line and progeny no.	Pod no. of		Means of S_1 progenies (1957)						
	Parent plants (1955) (open-pollination)	S_0 plants (1956) (tripping)	Flowers	Pods	Seeds	Per cent. flowers set	Seeds per 100 flowers	Per cent. flowers set	Seeds per 100 flowers
Ch 4R ₁ /1		13	108.2	5.4	9.0	5.0	8.2		
2/1		6	102.0	2.0	3.0	2.0	3.2		
3/1	31	11	100.2	3.0	5.2	3.0	5.3	4.4	8.5
4/1		6	101.0	14.0	36.5	13.9	36.1		
5/1		9	107.0	4.2	7.0	3.9	6.3		
1/2		2	109.0	4.0	6.0	3.7	4.8		
2/2		5	72.0	1.8	3.0	2.5	3.8		
3/2	24	10	100.8	0.6	1.6	0.6	1.5	1.6	2.5
4/2		2	101.4	1.2	1.2	1.2	1.3		
5/2		10	85.4	0.8	1.6	1.0	1.9		
1/3	24	8	106.0	0.6	1.0	0.6	0.9	1.9	3.9
4/3		10	106.8	3.4	7.2	3.2	6.9		
1/4		17	98.4	6.6	9.0	6.7	9.1		
2/4		20	104.6	5.2	7.0	4.0	5.8		
3/4	15	16	92.6	4.0	6.2	4.3	6.8	6.7	13.5
4/4		13	109.0	10.4	15.2	9.5	14.4		
5/4		6	106.3	9.3	17.0	8.7	15.9		
1/5		5	101.6	1.4	2.0	1.4	2.0		
2/5		6	136.6	4.8	4.0	3.5	3.1		
3/5	21	7	103.4	3.6	6.2	3.5	6.1	2.8	4.4
4/5		12	110.6	1.0	2.0	0.9	1.8		
5/5		8	100.8	4.6	9.0	4.6	9.0		
Mean	23.0	9.2	102.9	3.8	6.4	4.0	7.0	...	...

It will be observed that the mean number of pods, seeds, and seeds per pod, for the whole Ch 170 population has not been improved by the particular form of selection practised. However, two families stand out as consistently high pod and seed setters, namely, 9 and 21 (tables 4, 5), and of these No. 21 is extremely promising, but neither family could have been recognised in S_1 or S_2 as likely to give consistently self-fertile progeny.

It would appear that no general correlation exists between individual plants and their progenies with respect to pod and seed number.

4. INBREEDING OF CH 4

The original field population was analysed as fully as possible in 1955. Forty plants within the population were marked at random and the numbers of flowers and pods were recorded throughout the season.

TABLE 7

Analysis of variance of differences between lines and also between progenies with respect to seeds per 100 flowers

Component	N	Mean squares	F	Probability
Between lines . . .	4	242.0	20.1	<0.1 per cent.
Between progenies . .	22	153.8	12.7	<0.1 per cent.
Within progenies . . .	76	12.1	...	...
	102			

TABLE 8

Pod and seed setting in S_1 progeny plants, S_2 families and S_3 families of Ch 4

Progeny and family no.	S_1 plants (1957)		S_2 families (1958)			S_3 families (1959)		
	No. of		Mean no. of			Mean no. of		
	Pods	Seeds	Flowers	Pods	Seeds	Flowers	Pods	Seeds
4.1 (1)	13	35	59.4	3.7	9.5	71.1	4.5	9.5
(2)	15	38	67.2	5.3	11.9	55.0	8.0	18.5
1.2 (2)	2	3	203.7	1.7	2.7	83.0	0.8	1.3
(3)	10	15	135.6	4.3	7.4	63.8	3.6	7.0
4.4 (5)	14	18	111.9	4.8	9.1	65.2	5.9	10.1
5.4 (4)	19	30	90.1	2.9	4.6	67.7	3.2	4.9
2.5 (3)	8	11	75.2	4.8	8.8	54.5	4.9	9.1
Mean	11.6	21.4	106.2	3.9	7.7	65.8	7.7	8.6

The number of flowers per plant varied from 50-150 with a mean of 98.0. The pods had a much more restricted distribution, namely, from 5-50 per plant with a mean of 23.1. Between 10 and 50 per cent. of the total flowers set pods, the mean flowers set being 23.6 per cent.

Progenies were grown from each of the five random plants described in table 1 and allowed to set seed after tripping in an insect-proof glasshouse. The data on selfing this Ch 4 population are given in table 6.

Pod number although reduced in most S_0 plants was still high in some, particularly in those derived from Ch 4 R 4. In 1957, random progenies were grown from each original line and they were allowed to set seed unaided in an insect-proof glasshouse. Pod number was still further reduced, except in Ch 4 R 4 progenies and in line 4/1 where a considerable increase occurred. An analysis of the differences between progenies and lines on the basis of seeds set per 100 flowers is given in table 7.

Lines Ch 4 R 1 and Ch 4 R 4 are significantly better than the others and differences between progenies within lines are also significant, progenies 4/1, 4/4 and 5/4 being particularly self-fertile.

Progenies 4/1, 1/2, 2/4, 4/4, 5/4 and 2/5 were continued in 1958 and 1959, and all the available seed was sown up to a maximum of 20 per progeny. These plants were again allowed to set seed unaided in an insect-proof glasshouse; the number of flowers, pods and seeds per plant were recorded (table 8).

The mean numbers of pods and seeds again increased in 1959, also the percentage of flowers forming pods. This increased flower setting cannot be due to the elimination of self-sterile plants, as can be seen from the following figures :

Year	Generation	Per cent. flowers setting pods	Per cent. sterile plants
1955	Open-pollinated parents	23.6	0.0
1956	S_0 selfed plants (tripped)	7.3	5.6
1957	S_1 " "	3.7	19.4
1958	S_2 " "	5.1	2.1
1959	S_3 " "	11.7	10.4

Although the reduced number of flowers per plant in 1959 may be partly responsible for the relative increase in flower setting, nevertheless this improvement is a real effect and not a chance occurrence. This is shown by the analysis of the correlations of S_3 on S_2 family means for number of pods and seeds per plant. For pods $r = +0.91$ and for seeds $r = 0.94$, both correlation coefficients are highly significant ($P = 0.1$ per cent). Not only do the families and progenies differ significantly from each other in self-fertility but these differences appear to be inherited, and therefore are capable of improvement by selection. Some improvement in seed number per plant is shown but no conscious selection has been made for seed-setting on selfing. In fact it would appear that as soon as direct selection is made for seed-setting (as in Ch 170) the actual seed-set may be reduced.

5. DISCUSSION

The behaviour of the two populations Ch 4 and Ch 170 under inbreeding offers an interesting comparison. The families were grown alongside each other every year and the only difference between them

was that Ch 4 was based on unselected progenies in each generation while the Ch 170 population was subjected to intensive selection for high seed-set:

	S_0	Mean seed-set in each generation		
		S_1	S_2	S_3
Ch 170 . . .	13.3	5.4 (6.8)	11.0	11.4
Ch 4 . . .	13.8	6.4	7.7	8.6

The flowers in the S_0 generation were hand "tripped" and this accounts for the larger seed-set. In the S_1 generation the highly-selected Ch 170 progenies had a lower seed-set (5.4) than those where selection had been relaxed (6.8 seeds). Despite the intensive selection seed-set was only maintained in the S_3 generation of Ch 170 while the unselected Ch 4 progenies continued to improve in seed-set.

Genetic variability for seed-setting on selfing is undoubtedly present in the material since the lines here diverged on inbreeding (table 7) although the grand mean has remained little changed throughout. Sybenga (1958) has described an experiment in rye where a record was made of seed-setting on self-pollination during inbreeding. Seed-set improved in S_2 and S_3 generation but decreased in the S_4 and S_6 generations. Moreover, seed-set on selfing never exceeded that set after free pollination and only approached it in the S_3 . Similar situations were observed on inbreeding grasses and other forage crops (Wexelsen, 1952) and particularly in red clover (Thomas, 1955).

Thompson and Rees (1956) demonstrated that during inbreeding of rye some selection occurred for heterozygotes. Selection did not operate in favour of heterozygotes in general, but in favour of a particular heterozygous combination, indicating that heterozygosity in itself is not necessarily advantageous. It was not possible to rule out completely a recessive gene of major effect, but it was suggested that a more likely explanation was that of a superior balance of polygenes in that particular hybrid combination.

In part I of the present investigation (Rowlands, 1960) infertility at the zygotic level was explained in terms of homozygosis of deleterious recessive genes following inbreeding, and, moreover, that these genes were linked together in a balanced system. It is inevitable with only six linkage groups that other balanced combinations will be associated with these linked deleterious recessives and will contribute to the superiority of certain heterozygous combinations. The selective advantage in natural populations of the linkage within and between polygenic systems has been discussed by Mather (1953). Correlated responses to selection can be extensive under such conditions and can

give rise to true inertia (or homeostasis) but although they slow down, they do not finally prevent response to selection.

Evidence for dominance and non-allelic interaction of the genes controlling self-fertility was obtained from the diallel analysis of seed-setting in part I, and Jinks (1955) has related similar genetic situations in maize and other crops to close linkage in opposition of particular gene combinations. In such a system, inbreeding will fix the balanced combinations (Mather, 1953) and since the phenotypes determined by the different balanced combinations are alike they will be retained equally in the population. Effective segregation and recombination cannot occur in the absence of crossing, so that the balanced combinations will not be broken up despite the presence of genic differences. When the variability has been frozen in this way, change under directional selection is impossible and recombination must be induced by crossing over for any progress to take place in the population.

Breese (1956) has discussed assortative (*i.e.* like by like) mating in this context and concludes that "where genes controlling a character tend to be linked in opposition, assortative mating followed by selection, by avoiding the premature homozygosis and fixation resulting from inbreeding should maximise the chances of securing and ultimately fixing desirable recombinants". Such a programme of assortative mating and selection in beans might well result in the isolation of vigorous self-fertile lines in which a new internal chromosomal balance may be established.

The data presented by Williams and Gilbert (1960) show that such internal balance has been achieved unconsciously in the tomato during its change-over from outbreeding to inbreeding. Consequently, once the underlying genetic system has been discovered it is reasonable to suppose that a properly designed breeding programme should be able to complete quickly and effectively the change-over to inbreeding that may have begun naturally in any outbreeding species.

6. SUMMARY

1. The behaviour of pod and seed-set under self-pollination has been investigated during a programme of inbreeding.

2. Self-pollination was relatively ineffective in producing seeds, and selection for this character over three generations of inbreeding was not successful. Intensive selection for seed-set on self-pollination in one population had no marked effect, while in an unselected population seed-set appeared to improve slightly after three generations.

3. It is suggested that the presence of deleterious recessive genes, coupled with the development of close linkage in opposition of particular gene combinations, has produced a balanced system which directional selection alone is unable to break up.

4. Assortative mating followed by selection, by avoiding the fixation resulting from inbreeding, should maximise the chances of securing

and fixing desirable recombinants, and such a programme is recommended for the development of vigorous self-fertile lines not only in field beans but also in other outbreeding crops.

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