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Factors determining the performance of synthetics in *Vicia faba* L. 2. Syn-generation

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Summary

In the partially allogamous faba bean, yield and yield stability can be improved significantly by heterozygosity and heterogeneity. The commercial production of hybrid varieties for the full exploitation of heterosis is still unfeasible. Hence, the breeding of synthetic varieties has repeatedly been recommended. The present study aimed at investigating whether and to what extent effects due to heterozygosity and heterogeneity occur in such varieties, particularly in relation to Syn-generation. A sample of 36 inbred lines (*Vicia faba* L. *minor*) was used to generate several entries of different population structure, e.g. blends of inbred lines (= Syn-0), experimental synthetics of generations Syn-1 to Syn-4 and polycross progenies. In 1986 to 1991 these entries were evaluated together with their parental lines grown in pure stands in six series of multi-locational field trials in West Germany. The yield of the synthetics increased with successive Syn-generations and asymptotically approached its maximum by as early as generations Syn-2 or Syn-3. The yield increase was mainly caused by heterozygosity. In two synthetics the yield increase corresponded to about one-half to two-thirds of the mid-parent heterosis. Effects due to heterogeneity were small and mostly non-significant. In one out of three experiments significant effects due to seed source were observed which, however, did not alter the yield increase with successive Syn-generations. Hence, Syn-generations Syn-2 or Syn-3 may be sold to the farmer.

Introduction

Considerable mid-parent heterosis for grain yield of 27% to 76% has been reported in spring faba beans (Ebmeyer, 1988; Ebmeyer & Stelling, 1994; Esser & Stelling, 1992; Grotehusmann & Röbbelen, 1985; Link, 1988; Link et al., 1994a; Scheybal, 1988). As yet, however, due to the instability of the male sterility cytoplasms available (Bond, 1987), no hybrid variety has been released. The average degree of cross-fertilization of faba bean is about 30% to 60% (Bond & Poulsen, 1983; Link, 1990). Therefore, in presently released population varieties only part of the heterosis is used (Ebmeyer & Stelling, 1994).

Population varieties in faba bean are bred either as 'continued population varieties' (e.g. Bouwman, 1992) or as 'synthetic (population) varieties' (e.g. Bond, 1982; for nomenclature and definition of variety categories see Schnell, 1982). The levels of heterozygosity and heterogeneity of such varieties may differ considerably (Ebmeyer & Stelling, 1994) depending in particular on (a) the average degree of cross-fertilization, (b) the effective population size, and (c) the genetic distance among the parental components and/or their genetic constitution. All these factors are strongly related to the requirements for a high homogeneity within cultivars.

The yield and yield stability in faba bean are significantly improved by increasing levels of heterozygosity and heterogeneity (Link et al., 1994a; Stelling et al., 1994a). Few experimental data have been reported on the joint effect of heterozygosity and heterogeneity on the yield performance of faba beans as realized in population varieties and possibly soon (cf. Duc et al., 1992) in three-way or double hybrids. Concerning yield stability, both factors frequently do 'interact in the sense of diminishing returns' in several crops (Schnell & Becker, 1986; Léon, 1991; Stelling et al., 1994a).

Hence, the objective of the present study was to investigate the joint effects of heterozygosity and heterogeneity on yield and other agronomic traits in faba bean. For this purpose, the data of six series of field experiments were analysed. Special attention was given to successive multiplication generations of synthetics (= Syn-generations).

Material and methods

Thirty-six inbred lines derived randomly from the six German interminated faba bean population varieties 'Diana', 'Herra', 'Herz Freya', 'Kristall', 'Nixe', and 'Kleine Thüringer' by continuously selfing for at least eight generations were used. From all these lines or from a subset of eight inbred lines (four derived from 'Herz Freya' and four from 'Kristall'), entries with different population structures were developed and tested in six different series of field trials (= data sets) as indicated in Table 1 (cf. Stelling et al., 1994a; Link et al., 1994a):

a) inbred lines tested in pure stands (= lines; = P);
b) blends of four inbred lines each (= line blends; = Syn-0);
c) synthetics in generation Syn-1, Syn-2, Syn-3, and Syn-4;
d) blends of two hybrids each (- hybrid blends); and
e) polycross progenies.

In addition, two of the six source varieties, i.e. 'Herz Freya' and 'Kristall', were tested.

Seeds of inbred lines and F_1-hybrids were produced in bee-proof isolation cages, for the F_1 by hand crossing. For blending, equal numbers of seed per component were used. Line blends were also grown under open pollination in spatial isolation, either at Göttingen (data sets 1 to 3) or at Hohenheim (data sets 4 and 5; Table 1), to produce further synthetic generations. With the exception of the Syn-1 in data set 2 the seed lots of the different Syn-generations of each data set were all produced in one year in order to avoid effects due to seed source. The seed lots of the Syn-1 in data set 2 were produced two years earlier under unfavourable, cold and wet weather conditions. In several instances, the same Syn-generation was also produced in a different year. These seed lots were partly tested, too (Table 1). Polycross progenies were produced at Hohenheim in 1988 (Fleck & Ruckenbauer, 1989). Synthetics were mainly composed according to simultaneous anthesis. The composition of individual synthetics (A to L) is given in Table 2. Synthetics A and B consisted of lines exclusively derived from one variety, i.e. 'Herz Freya' or 'Kristall' (= intra-varietal synthetics). The same eight lines, two lines of each source variety, were used for synthetics C and D (= inter-/intra-varietal synthetics). Since synthetics C and D are connected to synthetics A and B by two lines, mean of (A + B) and (C + D) can be directly compared. For the production of hybrids, only lines of different source varieties were crossed. The line composition of hybrid blends was equal to that of synthetics C and D, respectively (cf. Stelling et al., 1994a).

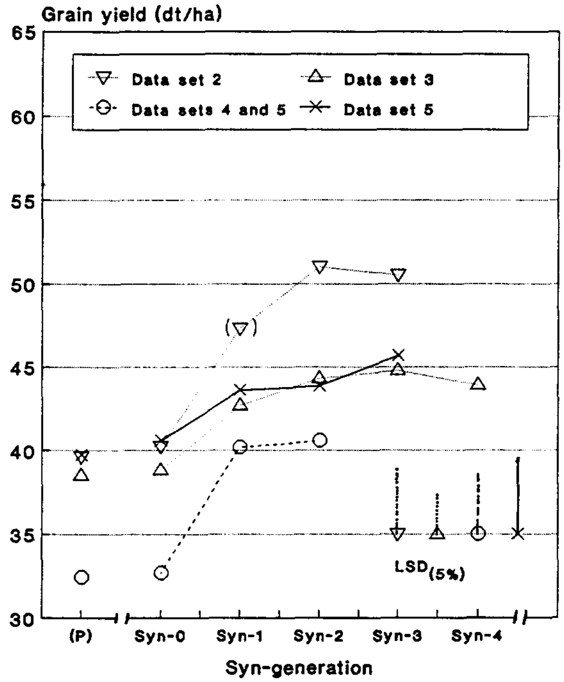

Fig. 1. Influence of the Syn-generation on grain yield of synthetics in faba bean in four series of field trials (data sets 2 to 5). For comparison, the mean performance of the parental components grown in pure stands (= P) is given (LSD for Syn-generation is given at p = 0.05 level).

Allocation of the entries of the six data sets is given in Table 1. Entries were tested in at least two environments in West Germany, with two to four replications each in the years 1986 to 1991. For data set 6, a split-plot design was used. The main plots consisted of two subplots, the parental inbred line and its respective

Table 1. Composition and allocation of entries of six different series of trial (= data sets)

Data set	Year	Number of Test sites	Replications per site	Population structures tested and number of entries (for Syn-1 to Syn-4, in addition, the year of seed production is given)
1	1989	3	2	8 inbreds, 4 inbred blends, 4 synthetics in Syn-2 (1988), 2 hybrid blends, and both source varieties
2	1990	4	2	Entries of data set 1 completed by 4 synthetics in Syn-1 (1987), Syn-2 (1989) and Syn-3 (1989)
3	1991	4	3	8 inbreds, 4 inbred blends, 4 synthetics in Syn-1 to Syn-4 (1990), Syn-2 (1988) and Syn-3 (1989; one test site only), and both source varieties
4	1989	3	4/3	36 inbreds, 9 inbred blends, 9 synthetics in Syn-1 (1988) and Syn-2 (1988)
5	1990	2/3	4/3	36 inbreds, 9 inbred blends, 9 synthetics in Syn-1 to Syn-3 (1989), Syn-1 (1988) and Syn-2 (1988)
6	1989	2	3	36 inbreds and their 36 respective polycross progenies

polycross progeny. For the other trials, the experimental layout was a lattice design. The plot size varied from 5.0 to 6.0 m^2 between sites. The average plant density among test sites varied between 24 and 32 plants/m^2. Whole plots were harvested. On a plot basis grain yield (in dt/ha), onset of flowering (days after 1^{st} January), maturity (days after 1^{st} January), plant length (in cm) standing ability (1: totally lodging; 9: upright standing), and thousand grain weight (in g) were recorded.

For statistical analysis, the lattice designs were analysed separately for each environment. Adjusted entry means were used for the subsequent analysis of variance over environments according to Cochran & Cox (1957, chapt. 14). The F-test was used to test the variance of experimental factors, whereby, for each data set, a completely random model was applied (Searle, 1971, chapt. 9). For statistical significance $^+$, *, and ** are used to indicate significances at the 10%, 5%, and 1% level of error probability, respectively. Mean values as well as minima and maxima of single entries are given (min. $\leq \times \leq$ max.).

Table 2. Composition of eleven synthetics (A–L) developed from 36 inbred lines derived randomly from the faba bean varieties 'Diana', 'Herra', 'Herz Freya', 'Kristall', 'Nixe', and 'Kleine Thüringer'

Synthetic	Components
A	HF17, HF18, HF23, HF24
B	KR25, KR27, KR31, KR32
C	HF17, HF23, KR25, KR31
D	HF18, HF24, KR27, KR32
E	DI02, HE16, KT43, KT47
F	DI03, DI06, HE11, KT48
G	HF19, KR26, NX33, NX35
H	DI07, DI08, HE14, KR30
I	HF22, NX38, NX39, KT46
K	DI01, HE09, HE10, KT43
L	HE15, NX34, NX40, KT41

Results

In all trials significant differences between entries were found. Heritability estimates of yield varied from 0.35 to 0.95 with a mean of 0.79 for single trials and from 0.68 to 0.96 with a mean of 0.82 for trial series. In each trial series the genotype × environment interaction proved to be highly significant for yield (data not shown).

The grain yield of the synthetics increased with successive Syn-generations and reached its maximum in generations Syn-2 (Fig. 1, data set 2) or Syn-3 (data sets 3 and 5). The yield increase was significant only from generation Syn-0 to Syn-1 (+ 8% to + 23%).

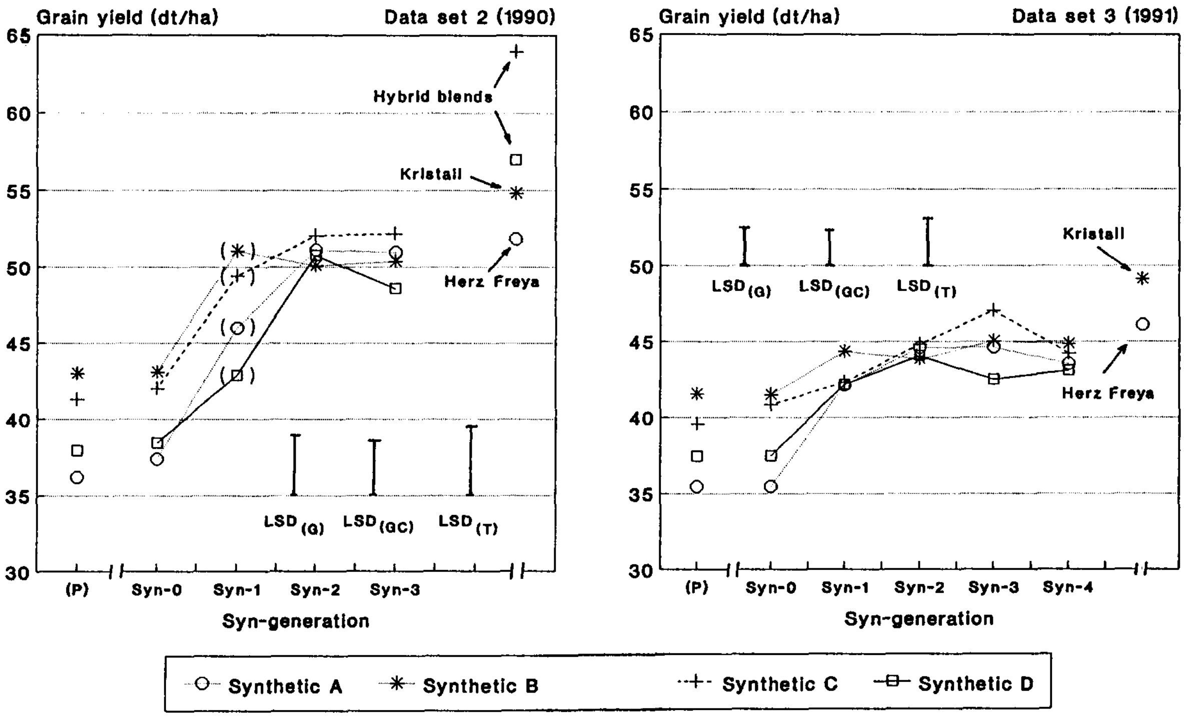

Fig. 2. Influence of the Syn-generation on grain yield of four faba bean synthetics (A–D; each averaged over four test sites in 1990 and 1991). For comparison, the mean performance of the parental components grown in pure stands (= P), the F_1-hybrid blends and the source varieties are given (LSD for Syn-generation (G), Syn-generation × line composition (GC) and entries (T) are given at p = 0.05 level).

In generation Syn-2 a further but small yield increase was observed (+ 1% to + 8%; Fig. 1). A similar trend was found for thousand grain weight and plant length (Table 3). There was a slight tendency towards earlier flowering and earlier ripening of, however, varying magnitude in most Syn-generations when compared with line blends (= Syn-0). The standing ability proved to be unaffected by synthetic generation.

Compared with the average performances of the lines in pure stands only small and mostly insignificant yield advantages of line blends (= Syn-0) were observed (Fig. 1, cf. Link et al., 1994a). The increase of yield in Syn-1 and higher Syn-generations, therefore, was predominantly caused by effects due to increasing heterozygosity. This is demonstrated in more detail for synthetics A to D in Fig. 2. Comparisons are made with the average yield of corresponding lines grown in pure stands (= P) as well as with the yield of the two hybrid blends and the two source varieties. If the effect of heterogeneity on yield in synthetics of generations Syn-1 to Syn-4 was similar to that in Syn-0 (= line blends; $+ 0.2\% \leq + 1.6\% \leq + 3.3\%$ in 1990, and $- 0.1\% \leq + 0.8\% \leq + 3.2\%$ in 1991), then the maximum yield increase due to the effects of heterozygosity was about $18.5\% \leq 27.9\% \leq 36.7\%$ in 1990, and $8.3\% \leq 16.8\% \leq 25.8\%$ in 1991. Compared with the mid-parent heterosis of the two hybrid blends (52% and 48%, respectively; data set 2, 1990), only one-half to two-thirds of this heterosis was exploited in synthetics C and D. Yield of the intra-varietal synthetics A and B was less than that of their corresponding source variety.

The analysis of variance for the effects of Syn-generation, line composition and environment on yield are given in Table 4. Most of the genotypic variation between the different synthetic stocks tested was caused by effects of the Syn-generation (data sets 1 to 4). The quadratic component for Syn-generation (G_q) proved to be highly significant, reflecting the decreasing yield increase at higher Syn-generations (Figs. 1 and 2). Except for data set 5, only about one-tenth to one-fourth of the genotypic variation resulted from differences in synthetic composition and interactions between synthetic composition and Syn-generations. In each data set the Syn-generation × environment interaction proved to be significant (data not shown).

Table 3. Effect of the Syn-generation on the agronomic performance of synthetics in faba bean in five series of field trials (data sets 1 to 5)

Data set	(No. of envs.)	Syn-generation (G)					$LSD_{(G)5\%}$
		0	1	2	3	4	
a) Onset of flowering (days)							
1	(2)	158.0		- 0.4			
2	(4)	155.6	- 0.2	- 1.2	- 1.1		0.9
3	(4)	168.1	+ 0.1	- 0.1	- 0.2	- 0.6	0.5
4 + 5	(5)	148.1	- 0.3	- 0.6			0.5
5	(2)	147.2	- 0.4	- 0.5	+ 0.1		0.6
b) Date of maturity (days)							
1	(3)	227.9		- 0.8			
2	(3)	226.5	- 0.0	- 0.1	+ 0.0		
3	(3)	231.5	- 0.8	- 0.7	- 0.2	- 0.3	1.0
4 + 5	(5)	214.8	- 0.4	- 0.3			0.5
5	(2)	216.6	+ 0.2	+ 0.2	+ 0.0		0.9
c) Plant length (cm)							
1	(3)	100.4		+ 2.6			
2	(4)	150.0	+ 3.4	+ 7.4	+ 8.5		5.7
3	(4)	139.0	+ 4.8	+ 6.6	+ 7.4	+ 5.2	2.7
4 + 5	(1)	158.0	+ 8.6	+10.7			3.8
5	(1)	158.0	+ 4.5	+ 3.9	+ 6.4		3.8
d) Standing ability (1: totally lodging; 9: upright standing)							
1	(2)	8.9		- 0.1			
2	(4)	6.6	- 0.0	+ 0.3	+ 0.4		1.1
3	(4)	8.1	+ 0.0	- 0.1	- 0.0	- 0.0	0.2
4 + 5	(4)	6.6	+ 0.0	- 0.0			0.4
5	(2)	4.9	- 0.1	- 0.0	- 0.2		1.4
e) Thousand grain weight (g)							
1	(3)	432		+ 30			
2	(4)	387	+ 15	+ 27	+ 37		16
3	(4)	403	+ 4	+ 21	+ 25	+ 30	16
4 + 5	(5)	399	+ 28	+ 25			16
5	(2)	419	+ 19	+ 16	+ 16		12

In Table 5 grain yield of lines, line blends, synthetics in generation Syn-1 and polycross progenies are given. Compared with the yield of the lines, polycross progenies exhibited a considerably higher yield than the synthetics in generation Syn-1.

For the synthetics of data sets 2, 3 and 5, additional seed lots of the generations Syn-1, Syn-2 and Syn-3 produced in a different year were evaluated for yield (cf. Table 1). Large and significant effects due to seed source, i.e, year of seed production, on yield were found only in one out of three experiments. In data set 5, an average effect of 14% in generation Syn-1 and 13% in generation Syn-2 was observed. Nevertheless, the shape of yield increase with successive Syn-generations proved to be similar to that observed for the other data sets shown in Fig. 1.

Discussion

The level of heterozygosity was the most important factor enhancing the yield in the faba bean. Effects due to heterogeneity seemed to be of minor importance. The yield of the experimental synthetics increased with successive Syn-generations and reached its maximum asymptotically in generations Syn-2 or Syn-3 (Figs.

Table 4. Analysis of variance for the effects of genetic composition and Syn-generation on grain yield of experimental synthetics in faba bean

Data set°	Sources of variation							
	Composition of synthetics (C)		Syn-generation (G)		Comp. × Gen. (C × G)		Environment (E)	
	df	c.v.	df	c.v.	df	c.v.	df	c.v.
1	(3)	0.5	(1)	8.3	(3)	#	(2)	86.5**
2	(3)	4.0+	(3)	38.2**	(9)	3.2+	(3)	38.6**
			G_l (1)	30.8**				
			G_q (1)	7.4**				
3	(3)	0.6+	(4)	4.2**	(12)	1.0**	(3)	91.3**
			G_l (1)	2.7**				
			G_q (1)	1.5**				
4 + 5	(8)	0.9	(2)	14.2**	(16)	1.1*	(4)	70.3**
			G_l (1)	11.2**				
			G_q (1)	3.0**				
5	(8)	#	(3)	7.6	(24)	18.2**	(1)	14.1+
			G_l (1)	6.9				
			G_q (1)	0.2				

°) Only considering those stocks of the experimental synthetics produced in the same environment;
df: Degrees of freedom; c.v.: Components of variance given in percent of the total variance:
$\sigma^2\text{total} = \sigma^2{}_C + \sigma^2{}_G + \sigma^2{}_{C\times G} + \sigma^2{}_E + \sigma^2{}_{E\times C} + \sigma^2{}_{E\times G} + \sigma^2{}_{C\times G\times E} + \sigma^2{}_e$;
G_l and G_q: Linear and quadratic component for Syn-generation; respectively;
Negative estimate.

1 and 2). Comparable experimental results have been reported by Bond (1987) in faba bean, and by Schuster et al. (1978) and Schuster (1982) in rapeseed and mustard. The observed yield increase, thereby, is in accordance with theory as elaborated by Busbice (1969), reviewed by Becker (1989), and specified for faba bean by Wright (1977), Link (1990) and Ederer (1991).

Assuming a linear relationship between performance and panmictic index (PI) or inbreeding coefficient (F = 1-PI), i.e. neglecting effects due to epistasis and competition, and assuming that effects due to heterogeneity are independent of the PI (cf. Link et al., 1994a; Stelling et al., 1994a), yield increase of synthetics in the first Syn-generations mainly depends on the number of parental components (k) and their degree of cross-fertilization (X). In the case of unrelated, completely homozygous inbred lines as source material and absence of dominance for the degree of cross-fertilization the following formulas for PI are valid in generations Syn-1 and Syn-2 (cf. Becker, 1989):

$$PI_{(k;Syn-1)} = 1 - F_{(k;Syn-1)} = (1 - 1/k)\,X \qquad (1)$$

$$PI_{(k;Syn-2)} = 1 - F_{(k;Syn-2)}$$
$$= 1 - (1 - X)/2 + X/k + [(1 - X)/2][1 - (1 - 1/k)X] \qquad (2)$$

At Hohenheim, averaged over the four lines of synthetics C and D, respectively, degrees of cross-fertilization of 49.8% and 56.2% were recorded in three years (cf. Link et al., 1994a). If we assume that these results approximately hold true for Göttingen in 1987 to 1989, by using equations (1) and (2) and considering the mid-parent heterosis for yield, expected increments of yield can be calculated for synthetics C and D and compared with the observed ones (Table 6). The expected yield increase in generation Syn-1 proved to be larger than the observed ones. This probably resulted from seed source effects caused by the unfavourable seed production conditions in 1987 (see Material and methods). In generation Syn-2, however, the predicted yield advance calculated by means of equation (2) proved to

Table 5. Comparison between pure stands of inbred lines, corresponding polycross progenies, line blends (= Syn-0) and synthetics in Syn-1 for grain yield (dt/ha; taken from data sets 4 and 6; seed lots of all entries were produced at Hohenheim in 1988)

Test site	Inbred lines (n = 36)	Polycross progenies (n = 36)	Synthetics in Syn-0 (n = 9)	Synthetics in Syn-1 (n = 9)
Neckarmühlbach	32.3	41.8	31.1	38.5
(Rel.)	*100*	*129*	*96*	*119*
Hohenheim	24.9	32.9	26.1	31.0
(Rel.)	*100*	*132*	*105*	*124*

be smaller than the observed one. Differences between expected and observed values in Syn-2 would become even larger if a lower degree of cross-fertilization of F_1-hybrids compared with their parental inbreds (Link, 1990) was considered.

Deviations of observed values from expected ones may be caused by either different actual degrees of cross-fertilization, differences in the rate of seed multiplication (e.g. hybrids exhibit a higher rate than their respective inbreds), and/or effects of competition between plants of different heterozygosity levels, i.e. hybrids vs. inbreds in generation Syn-1, and hybrids vs. inbreds vs. partial inbreds in generation Syn-2; the latter are described by Link et al. (1994a) as effects due to 'heterogeneity for the individual inbreeding coefficient'.

There is clear evidence in faba beans for considerable variation in the degree of cross-fertilization due to effects of the year (Steuckardt et al., 1985), location (Link et al., 1994b) and genotype × environment interaction (Link et al., 1994a, b). Few data exist as to whether and to what extent grain yield may be altered by competition between plants of different heterozygosity levels, in the sense that in field stands '. . . containing genotypes varying in yield potential due to differences in heterozygosity level the more vigorous (hybrid) plants crowd out (particularly in forage crops) and/or compensate for the lower yielding (selfed) components of the population' (see Carnahan & Paden, 1967; Gallais, 1990, chap. 4.4; remarks in parentheses are added by us). Considering these phenomena the yield performance of a synthetic population derived from k inbred lines depends on:

a) the average *per se* performance of the parental inbreds

b) the average degree of cross-fertilization;

c) the average effect of heterozygosity;

d_1) and d_2) the average effects of heterogeneity between genotypes being similar or different in their PI; and

e) the interaction between heterozygosity and heterogeneity.

For grain yield, positive as well as negative effects due to 'heterogeneity for the individual inbreeding coefficient' have been reported (Hühn & Schuster, 1975), in rapeseed; Norrington-Davies, 1972, in barley; Link et al., 1994a, in faba bean). Hence, hybrids are not *ipso facto* strong competitors. Data on the significance of this specific type of heterogeneity are valid in each type of hybrid variety containing proportions of parental plants, e.g. chance-hybrids in forage crops (Bertling, 1993) and hybrid varieties produced either by means of an imperfect CMS system or by mixing pollinator and CMS plants.

The inter-varietal synthetics C and D, respectively, utilised approximately 46% and 66% of the full heterosis that is exploitable in hybrid varieties (Fig. 2). Similar data were found by Ebmeyer & Stelling (1994) in three open pollinated faba bean varieties. Nevertheless, yield of the intra-varietal synthetics A and B did not reach the yield level of their respective source varieties (Fig. 2). This may mainly be a consequence of (1) a higher inbreeding coefficient in the synthetic due to the low number of lines used and (2) due to the fact that this was not counterbalanced, since the lines were derived without selection from the source varieties. The large genotypic variability found within open pollinated faba bean varieties by Poulsen (1979) and Ebmeyer & Stelling (1994) corroborates these conclusions.

Polycross progenies are similarly composed to the synthetics in generation Syn-1: both consist of selfed inbreds and F_1-hybrids. If based on the same set of inbred lines, differences in the performance between such related types of variety should, therefore, mainly result from differences in the frequency of hybrid plants. In generation Syn-1 this frequency is determined by the number of parental components (k) and their degree of cross-fertilization (X; see equation 1). Since k = 36 for the polycross progenies and k = 4 for the synthetics, the yield of the polycross progenies proved to be considerably higher than that of the related synthetics in Syn-1 (Table 5).

Theoretical as well as experimental results clearly showed that in faba bean synthetic varieties may be sold for commercial production already in generations Syn-2 or Syn-3. However, inbred components

Table 6. Expected and observed increments in yield (dt/ha) of two experimental synthetics in generations Syn-1 and Syn-2 compared with generation Syn-0

Data set	Synthetic	Syn-1		Syn-2	
		Expected (Eq.1)[a]	Observed	Expected (Eq.2)	Observed
1 + 2	C	–		+ 7.98	+ 11.09
	D	–		+ 7.52	+ 8.06
2	C	+ 8.18	+ 7.40	+ 10.24	+ 10.04
	D	+ 7.82	+ 4.44	+ 9.54	+ 12.34

[a] Equation applied for calculation of expected values.

are mostly maintained in small quantities, so that due to the low multiplication rate at least one more generation of multiplication is required. The experimental data of Bond (1982) revealed that yield did not change from generations Syn-4 to Syn-8. Nonetheless, small reductions in yield may occur due to natural selection and/or negative heterosis regarding the degree of cross-fertilization (for the last see Link, 1990; Ederer, 1991). In order to achieve the maximum yield in farm crops the level of cross-fertilization should be increased in the generation before commercialization (Wright, 1977; Link et al., 1994b), e.g. by the introduction of honey bees. Value of seed source of faba bean synthetics may, therefore, be considerably affected by genetic factors (cf. Stelling et al., 1994b). Similarly, for the selection of components for synthetic varieties other than a favourable agronomic performance, some emphasis should be given to a high degree of cross-fertilization (Link, 1990; Ebmeyer, 1988). Further progress in yield can be expected if components derived from different heterotic groups are combined in synthetic varieties. However, the level of phenotypic variation within such varieties may become large. Therefore, it should be reconsidered whether homogeneity for variety registration should no longer be demanded from the synthetic variety but from its parental components.

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