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Mean, genetic variance, and usefulness of selfing progenies from intra- and inter-pool crosses in faba beans (*Vicia faba* L.) and their prediction from parental parameters

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Abstract Determining the genetic potential of a base population from the properties of their parental lines would improve the efficiency of a breeding program. In the present study, we investigated whether the means of the parents and the genetic distance determined from RAPD data (GD) or multivariate analysis (Mahalanobis D^2), mid-parent heterosis (MPH), and the absolute difference between means of the parents ($|P_1 - P_2|$) can be used for predicting the means and genetic variances ($\hat{\sigma}_g^2$) of $F_{3:4}$ lines derived from different crosses in faba beans. The material comprised 18 intra- and 18 inter-pool crosses among lines from the Minor, Major, and Mediterranean germplasm pools. Fifty $F_{3:4}$ lines from each cross were evaluated for days to anthesis, plant height, seeds per plant, and seed yield in German (GE) and Mediterranean (ME) environments. GD estimates between parent lines ranged from 0.38 to 0.58, while D^2 ranged from 45.5 to 134.7. Correlations between means of the parents and $F_{3:4}$ lines were highly significant for most traits. Estimates of σ_g^2 for all traits showed non-significant correlations with MPH, $\widehat{GD}$, D^2. In one ME, $|P_1 - P_2|$ had significant associations with $\hat{\sigma}_g^2$ for seed yield and days to anthesis. The predicted usefulness of crosses, defined as the sum of the population mean and selection responses, was most closely associated with the means of $F_{3:4}$ lines. We conclude from this study that the means of $F_{3:4}$ lines can be predicted from the means of the parents, whereas the prediction of genetic variance is still an unsolved problem

Key words *Vicia faba* L. · RAPD · Mahalanobis genetic distance · Usefulness · Genetic variance · Mid-parent heterosis

Introduction

The development of superior inbred lines transgressing the performance of their parents, or combining desirable attributes from them, are the main goals in crop-improvement programs. Commonly, F_2 or backcross populations from crosses of elite lines are used as source materials for this purpose. A large number of crosses are discarded after preliminary evaluation for *per se* or testcross performance. If breeders could identify promising crosses or source populations at an early stage of a breeding program from the properties of the parent lines, they could concentrate their efforts and resources on a few promising crosses with a large number of progenies.

Schnell (1983) devised the usefulness concept to assess the breeding prospects of base populations. Accordingly, the "usefulness" $U(\alpha)$ of a cross is defined as:

$$U(\alpha) = \mu + \Delta G(\alpha), \tag{1}$$

where μ denotes the population mean of all possible lines derivable from a particular cross without selection, and $\Delta G(\alpha)$ is the predicted selection response when selecting the upper α% fraction of these lines with regard to a given selection criterion. Since $\Delta G(\alpha)$ depends on the heritability and genetic variance

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(σ_g^2), Schnell's usefulness concept accounts for both the mean and genetic variance of the source population. This concept went beyond a similar proposal of Jinks and Pooni (1976), who estimated the probability that inbred lines from a cross exceeded a given threshold value, assuming that the broad-sense heritability is equal to unity.

Determining the mean performance and genetic variance among a large number of segregating progenies by field testing is both very tedious and resource consuming. According to quantitative genetic theory, the population mean μ can be predicted from the mid-parent value in the absence of epistasis (Melchinger 1987). Since the genetic variance depends on polymorphic loci segregating in a cross, various measures of genetic distance between parents have been proposed as a predictor of σ_g^2. Most frequently used are the coefficient of parentage, multivariate analysis of quantitative traits, and molecular markers such as RFLPs, AFLPs, RAPDs, or SSRs. Heterosis in crosses also provides an indirect measure of the genetic diversity between parental lines (Cowen and Frey 1987).

Studies concerning the prediction of σ_g^2 in source populations are scanty and with inconsistent results. Bhatt (1973) found that the genetic variance among $F_{4:5}$ lines in wheat increased with increasing genetic distance of their parents as determined by multivariate analysis. In studies with oats (Souza and Sorrels 1989, 1991) and soybean (Manjarrez-Sandoval et al. 1997), the coefficient of parentage proved to be the best predictor of σ_g^2. Genetic distance, measured by isozymes and morphological markers, was a useful predictor of σ_g^2 among F_5 lines derived from 72 crosses in *Pisum sativum* (Sarawat et al. 1994). In contrast, Moser and Lee (1994) found no correlation between various measures of genetic distance and σ_g^2 among progenies derived from a set of crosses between oat lines. Likewise, Kisha et al. (1997) concluded that neither the genetic distance estimated by RFLP markers nor the coefficient of parentage can accurately predict the genetic variance among lines in different crosses of soybean.

In the present study we explored the possibilities of predicting the components of Schnell's usefulness among crosses of unrelated lines from the same as well as different germplasm pools of faba bean (*Vicia faba* L.). The objectives were to predict, in intra- and inter-pool crosses: (1) the mean performance of $F_{3:4}$ lines from the mean of their parents ($\bar{P}$), ad (2) the genetic variance among $F_{3:4}$ lines from mid-parent heterosis and three measures of parental genetic distance estimated from molecular markers as well as qualitative and quantitative traits. In addition, we assessed the relative importance of differences in the means (μ) versus the selection response $\Delta G(\alpha)$ for the ranking of crosses according to their usefulness $U(\alpha)$ at two selection intensities.

Materials and methods

Genetic materials

Twenty inbred lines belonging to the Minor, Major, and Mediterranean germplasm groups of *V. faba* L. were used in the present study. Cultivation of the first two groups is restricted to Central and north-western Europe, while the latter group is grown primarily in southern Europe and northern Africa. These lines were chosen as representative samples of the respective germplasm pools and were generated from their progenitor varieties by single-seed descent. The Minor and Major lines descend from commercially used varieties from Germany, Great Britain, France and The Netherlands, whereas the Mediterranean lines were mainly chosen from ICARDA's pure-line collection and originated from various countries around the Mediterranean sea. A subset of 11 lines comprising three Minor, three Major, and five Mediterranean lines was crossed with a subset of nine lines, comprising three lines from each germplasm group, according to a factorial mating design, to produce a total of 99 F_1 crosses in both reciprocal forms. A detailed description of the lines and their 99 F_1 crosses was given by Link et al. (1996). In each of the 99 F_1 crosses, 50 plants were selfed in isolation cages to prevent cross pollination by insects. From these 99 crosses in the F_2 generation, 18 intra-pool (Minor × Minor, Major × Major, and Mediterranean × Mediterranean) and 18 intra-pool (Minor × Major, Minor × Mediterranean, and Major × Mediterranean) crosses were selected based on their mid-parent heterosis for seed yield determined in trials conducted in 1992 at San Biagio, Italy (for details see Link et al. 1996). From each each of the six crossing groups, two crosses with high, medium, and low heterosis were selected. Fifty F_2 plants from each cross were selfed by single-seed descent and the resulting F_3 plants were again selfed to produce 50 $F_{3:4}$ lines. In total 1800 $F_{3:4}$ lines across all 36 crosses were produced.

Field evaluation

The $F_{3:4}$ lines and their parental inbreds were evaluated in three trials: San Biagio (Italy) in 1995, Tadla (Morocco) in 1996, and Hohenheim (Germany) in 1996. The first two sites represent typical Mediterranean environments (ME), whereas the latter site represents a German environment (GE) and is typical for Central Europe. The experiment was conducted as a split-plot design with main plots arranged as a 6 × 6 lattice in two replications. Main plots consisted of crosses, while sub-plots comprised 50 $F_{3:4}$ lines of a particular cross. In addition, the 20 parental inbreds were evaluated in a randomized complete block design using four replications. To minimize the experimental error, the trial of the inbred lines was planted adjacent to the first replication of the trial for the $F_{3:4}$ lines. The experimental unit in all experiments was a single row, 1-m long, consisting of ten plants. Sowing was done on 12 December 1994 at San Biagio, 6 December 1995 at Tadla, and 10 April 1996 at Hohenheim. Precipitation during the relevant season for faba beans was 310, 450, ad 411 mm m^{-2} in the three environments, respectively. The crop duration was almost 4 weeks longer in the ME than in the GE. At Hohenheim, lodging was prevented by a mesh net stretched over the trial, whereas no lodging occurred in the ME. Standard crop production and protection treatments (fertilization, weeding, insect and pest control) were applied throughout all trials. The traits studied were days to anthesis, plant height (in cm) at maturity, number of seeds per plant, and seed yield (in g) per plant. At Tadla only yield data were recorded.

Statistical analyses

For each environment, the trait observations for the 50 $F_{3:4}$ lines were averaged in each cross and replication. Ordinary lattice analyses of variance were performed on these averages to calculate the adjusted "entry" means for each of the 36 crosses. The sums of squares for crosses (35 *df*) were subdivided into orthogonal contrasts among groups of crosses (5 *df*) and crosses within each group ($5 \times 6 = 30$ *df*) as described by Link et al. (1996). Repeatability for means ($\bar{F}_{3:4}$) of individual crosses was calculated from the lattice analysis. For the 20 parental inbreds, an analysis of variance for a randomized complete block (RCB) design was used to calculate means and repeatabilities. *F*-tests were used to test the significance of differences among means of parents ($\bar{P}$) as well as among the $\bar{F}_{3:4}$ of different crosses.

The 50 $F_{3:4}$ lines were analysed separately for each cross and environment using the analysis of variance for a RCB design. The genetic variance σ_g^2 was estimated as:

$$\hat{\sigma}_g^2 = (MS_{F_{3:4}} - MS_e)/r, \qquad (2)$$

where $MS_{F_{3:4}}$ refers to the mean squares due to $F_{3:4}$ lines, MS_e denotes the error mean squares pooled across all 36 crosses, and r is the number of replications. Heterogeneity of $\hat{\sigma}_g^2$ among the six crosses within a crossing group as well as among the average $\hat{\sigma}_g^2$ in the six crossing groups was tested using Bartlett's test criterion (Snedecor and Cochran 1980).

Estimation of predicted selection response and usefulness

The predicted selection response (ΔG) for selection intensities $\alpha = 1\%$ and $\alpha = 20\%$ were calculated for each cross and each environment by the following formula (Falconer 1981, p 175):

$$\Delta G(\alpha) = k_\alpha \hat{\sigma}_g \hat{h}, \qquad (3)$$

where k_α is the standardized selection differential for selection intensity $\alpha\%$, $\hat{\sigma}_g$ is the genetic standard deviation, and $\hat{h}$ is the square root of heritability. The latter was calculated as

$$\hat{h}^2 = \hat{\sigma}_g^2/(\hat{\sigma}_g^2 + \hat{\sigma}_e^2/r), \qquad (4)$$

where $\hat{\sigma}_e^2$ is the error variance pooled over all 36 crosses. The predicted selection response was used to calculate the usefulness $U(\alpha)$ according to eqn. (1).

Estimation of midparent heterosis

Data for the F_1 performance and mid-parent heterosis in German and Mediterranean environments were taken from trials conducted in 1992–1993 (for details see Link et al. 1996). The absolute mid-parent heterosis (MPH) was calculated across seven Mediterranean and two German environments as the difference between the F_1 performance (mean of both reciprocal crosses) and the mean performance of the two parents.

Estimation of genetic distance

Genetic distance (GD) based on RAPDs

Genetic distances between the 20 parental lines determined by RAPD markers were taken from Link et al. (1995). Briefly 59 random primers were used for DNA amplification by the polymerase chain reaction (PCR). DNA amplification products were analysed by electrophoresis in 2.5% agarose gels and visually scored for the presence or absence of amplification products (bands) at identical positions on the gel. Pairwise comparisons of lines for both unique and common bands at a particular gel position were used to calculate genetic distance (GD) estimates according to Jaccard (1908):

$$\widehat{GD}_{ij} = (N_i + N_j)/(N_{ij} + N_i + N_j). \qquad (5)$$

Here, N_i is the number of bands in line i and not in line j, N_j is the number of bands in line *J* and not in line i, and N_{ij} is the number of bands present in lines i and j. Thus, $\widehat{GD}$ ranges between 0 and 1 and reflects the proportion of the gel positions with bands in only one of both lines relative to the total number of gel positions with bands occurring in this same pair.

Genetic distance based on morphological traits (D^2)

Data on (1) 53 qualitative and quantitative traits (comprising 22 yield and yield component traits, 15 leaf, seed, and pod characteristics, 11 traits related to growth habits and duration, and five flower morphology and color traits), (2) ten traits with highest heritability, and (3) six traits having high correlations with yield, were used for multivariate analyses to obtain three estimates of Mahalanobis distance (D^2) as the squared Euclidian distance between the principal coordinate scores (Schill et al. 1997). Correlations between all three measures of D^2 were very high (>0.80). Therefore, only estimates of D^2 based on the 53 traits were used for further statistical analyses.

Estimation of correlation coefficients

For each trait and each environment, simple correlations (*r*) were calculated separately across the three intra- and three inter-pool crossing groups between the means of the parents ($\bar{P}$) and $F_{3:4}$ lines ($\bar{F}_{3:4}$) derived from each cross. Fisher's *Z* transformation, as described by Snedecor and Cochran (1980), was used for pooling correlations across intra-pool and inter-pool crosses, when the χ^2 test of heterogeneity indicated homogeneity of the correlations for the three crossing groups. A similar procedure was applied to calculate correlations of: (1) $\hat{\sigma}_g^2$ with the estimates of GD, Mahalanobis D^2, MPH, and absolute difference between means of the parents ($|P_1 - P_2|$), and (2) predicted usefulness $U(\alpha)$ with the estimates of $\bar{P}$, $\bar{F}_{3:4}$, $\hat{\sigma}_g^2$, and $\Delta G(\alpha)$.

Results

Variation for agronomic traits

Means

The average seed yield of the parents and $F_{3:4}$ lines across all 36 crosses was highest at Hohenheim (18.3 g) followed by Tadla (10.4 g) and San Biagio (2.9 g) (Table 1). Significant ($P < 0.01$) differences were observed among crosses within all groups and among averages of crossing groups for the means of the parents ($\bar{P}$) and $F_{3:4}$ lines ($F_{3:4}$) for all traits at all three locations. In all environments, the means of parents and $F_{3:4}$ lines for seed yield averaged across intra-pool crosses did not differ significantly from those of inter-pool crosses. In the ME, the average yield of parents and $F_{3:4}$ lines from the Mediterranean intra-pool crosses was significantly higher than that of the Minor and Major intra-pool crosses, while the reverse was true in the GE. Among the inter-pool crosses, the mean yield of parents and $F_{3:4}$ lines was higher in

Table 1 Estimates of means of parents ($\bar{P}$) and $F_{3:4}$ lines ($\bar{F}_{3:4}$), and genotypic variance ($\hat{\sigma}_g^2$) for seed yield (g plant^{-1}) among the 50 $F_{3:4}$ lines, derived from each of 36 faba bean crosses evaluated in two Mediterranean environments (San Biagio and Tadla) and one German (Hohenheim) environment, averaged over the six crosses within each crossing group

Crossing group	San Biagio			Tadla			Hohenheim		
	$\bar{P}$	$\bar{F}_{3:4}$	$\hat{\sigma}_g^2$	$\bar{P}$	$\bar{F}_{3:4}$	$\hat{\sigma}_g^2$	$\bar{P}$	$\bar{F}_{3:4}$	$\hat{\sigma}_g^2$
Minor × Minor	1.02	1.16	0.17	4.78	5.81	2.96	20.70	20.10	14.26
Major × Major	2.79	3.21	0.58	8.29	8.97	1.28	20.25	23.26	13.39
Mediterranean × Mediterranean	4.88	5.13	0.79	19.42	15.20	9.48	1314	12.29	16.62
Minor × Major	2.25	2.78	0.57	7.26	8.53	4.60	21.27	24.47	12.89
Minor × Mediterranean	2.92	3.91	0.62	10.99	10.31	12.02	15.91	17.67	11.42
Major × Mediterranean	3.44	4.42	0.60	11.90	10.21	13.23	16.93	19.68	12.31
Mean of intra-pool crosses	2.89	3.16	0.49	10.83	9.99	4.59	18.01	18.54	14.17
Mean of inter-pool crosses	2.87	3.70	0.60	10.05	9.68	9.25	18.04	20.61	12.21
Overall mean	2.88	3.43	0.54	10.44	9.83	6.92	18.33	19.58	13.19
LSD5%[a]	1.64	0.72	–	8.22	2.34	–	7.13	3.8	–
Repeatability (%)	89.49	90.73	–	85.67	64.97	–	78.15	89.00	–

[a] LSD 5% is for comparing the average $\bar{P}$ and $\bar{F}_{3:4}$ of different crossing groups

Major × Mediterranean crosses and in the ME and Minor × Major crosses in the GE as compared to the other two groups.

The means of parents and $F_{3:4}$ lines for plant height and seeds per plant were higher at Hohenheim than at San Biagio, while the reverse was true for days to anthesis (Table 2). In both ME and GE, the means of intra-pool crosses for parents and $F_{3:4}$ lines did not differ significantly from those of inter-pool crosses for these three traits. At San Biagio, highest means of parents were found in intra-pool crosses of Minor germplasm for days to anthesis and plant height, and of Mediterranean germplasm for seeds per plant. The intra-pool crosses of Minor germplasm also had the largest means for parents and $F_{3:4}$ lines for these three traits at Hohenheim.

Genetic variance among $F_{3:4}$ progenies ($\hat{\sigma}_g^2$)

Bartlett's test revealed heterogeneity ($P < 0.01$) for $\hat{\sigma}_g^2$ among the six crosses in each crossing group as well as between the average $\hat{\sigma}_g^2$ of the six crossing groups for all four traits and three locations (Tables 1 and 2). Averaged across all 36 crosses, the mean σ_g^2 among $F_{3:4}$ lines for seed yield was highest at Hohenheim and lowest by far at San Biagio. Inter-pool crosses had a significantly higher average $\hat{\sigma}_g^2$ for all traits in the ME, and for plant height and days to anthesis in the GE, than did the intra-pool crosses. For other traits, the trend was the reverse in the GE. Means of $\hat{\sigma}_g^2$ across the six crosses within a crossing group for seed yield were high in Mediterranean intra-pool crosses at San Biagio and Hohenheim, as well as in Major × Mediterranean inter-pool crosses at Tadla. Considerable variation in the estimate of σ_g^2 was found among the six crosses within all intra- and inter-pool crossing groups at Hohenheim and Tadla.

The means and ranges for $\hat{\sigma}_g^2$ were high for plant height and seeds per plant at Hohenheim and for days to anthesis at San Biagio (Table 2). In the latter environment, inter-pool crosses had the highest mean $\hat{\sigma}_g^2$ for days to anthesis. For individual crossing groups, the largest mean of $\hat{\sigma}_g^2$ was found in Minor × Major crosses for days to anthesis and plant height at Hohenheim, and in Minor × Mediterranean crosses for plant height and seeds per plant at San Biagio.

Predicted selection response (ΔG) and usefulness (U)

The estimates of ΔG and U for seed yield at two selection intensities were very high at Hohenheim compared to San Biagio and Tadla (Table 3). Under both selection intensities, the estimates of ΔG as well as U in most of the intra-pool crosses were similar to those of inter-pool crosses in all three environments. The Mediterranean intra-pool crosses at San Biagio and Hohenheim, and Major × Mediterranean inter-pool crosses at Tadla, had comparatively higher estimates of ΔG for seed yield than other crossing groups. The predicted usefulness (U) was highest for Mediterranean intra-pool crosses in the ME, and for inter-pool crosses of type Minor × Major in the GE, irrespective of the selection intensity α. Estimates of U at both selection intensities were lowest in Minor intra-pool crosses in the ME and Minor × Mediterranean inter-pool crosses in the GE.

Estimates of genetic distance between parent lines

Genetic distance (GD) based on RAPDs

Estimates of GD between the parents of 36 crosses ranged from 0.38 for the cross Fel × CEx of Major

Table 2 Estimates of the mean of parents ($\bar{P}$) and $F_{3:4}$ lines ($\bar{F}_{3:4}$), and genotypic variance ($\hat{\sigma}_g^2$) among the 50 $F_{3:4}$ lines, derived from each of 36 faba bean crosses for days to anthesis, plant height and seeds per plant at two environments, San Biagio, Italy, and Hohenheim, Germany, averaged over the six crosses within each crossing group

Crossing group	San Biagio			Hohenheim		
	$\bar{P}$	$\bar{F}_{3:4}$	$\hat{\sigma}_g^2$	$\bar{P}$	$\bar{F}_{3:4}$	$\hat{\sigma}_g^2$
			Days to anthesis (days)			
Minor × Minor	112.7	113.7	17.2	69.3	69.0	2.8
Major × Major	92.7	91.9	1.4	62.2	59.7	1.1
Mediterranean × Mediterranean	94.0	93.3	1.4	62.5	65.5	2.8
Minor × Major	100.5	98.0	22.9	65.1	62.8	8.6
Minor × Mediterranean	101.2	97.6	9.2	65.6	64.7	4.7
Major × Mediterranean	94.0	93.4	3.2	63.1	61.5	4.9
Mean of intra-pool crosses	99.8	99.6	6.7	64.7	64.1	2.2
Mean of inter-pool crosses	98.6	96.3	11.7	64.6	63.0	6.1
Overall mean	99.2	97.9	9.2	64.6	63.5	4.1
LSD5%[a]	1.8	1.7	–	4.9	1.4	–
Repeatability (%)	99.5	99.4	–	80.1	97.6	–
			Plant height (cm)			
Minor × Minor	54.2	49.6	10.0	139.8	163.3	32.3
Major × Major	41.0	40.1	5.7	116.6	100.6	11.3
Mediterranean × Mediterranean	41.5	40.0	6.0	98.4	80.4	46.1
Minor × Major	47.5	45.9	9.0	128.1	133.1	67.4
Minor × Mediterranean	47.4	46.1	14.5	122.0	118.1	59.7
Major × Mediterranean	41.5	40.3	4.7	118.9	99.2	41.1
Mean of intra-pool crosses	45.6	43.1	7.2	118.3	114.7	29.9
Mean of inter-pool crosses	45.5	44.1	9.4	123.0	116.8	56.1
Overall mean	45.5	43.6	8.3	120.6	115.7	43.0
LSD5%	5.7	3.8	–	34.9	10.5	–
Repeatability (%)	93.3	87.8	–	63.3	98.5	–
			Seeds per plant (number)			
Minor × Minor	3.6	4.2	2.0	59.0	57.2	108.7
Major × Major	4.6	4.8	1.1	27.4	26.9	16.2
Mediterranean × Mediterranean	10.8	11.4	2.1	35.4	31.6	89.5
Minor × Major	4.8	6.2	1.9	44.1	44.0	73.2
Minor × Mediterranean	7.0	10.1	3.8	43.2	44.6	98.8
Major × Mediterranean	7.3	8.3	1.7	33.7	33.9	26.0
Mean of intra-pool crosses	6.3	6.8	1.7	40.6	38.6	71.6
Mean of inter-pool crosses	6.4	8.2	2.5	40.3	40.9	65.0
Overall mean	6.3	7.5	2.1	40.4	39.7	68.3
LSD5%	3.0	2.0	–	16.9	8.1	–
Repeatability (%)	92.8	94.5	–	89.6	92.8	–

[a] LSD5% is for comparing means of crossing groups

germplasm to 0.58 for the crosses H20S × Pel and SCI × Giz of the type Minor × Mediterranean (Table 4). The parents of inter-pool crosses had a higher average $\widehat{GD}$ than the parents of intra-pool crosses. Minor × Mediterranean inter-pool crosses had the highest (0.55), and Major × Major intra-pool crosses had the lowest (0.44), mean $\widehat{GD}$ values. A comparatively small range in $\widehat{GD}$ values between the parents of the six crosses was observed in all crossing groups.

Mahalanobis distance (D^2)

Estimates of mean D^2 between parents of the inter-pool crosses were higher than those of intra-pool crosses and ranged from 104.6 to 134.7 and from 45.5 to 67.7, respectively (Table 4). Within intra- and inter-pool crosses, parents of the Major × Major and Minor × Major crosses had highest estimates of D^2. Parents of the cross K25 × SCI from the Minor germplasm had the lowest D^2 (27.9), and parents of the cross SCI (Minor) × Giz (Mediterranean) had the highest D^2 (173.8), value. A wide range in D^2 values was found between parents of the six crosses within each group, particularly for the Minor intra-pool crosses and the Minor × Mediterranean inter-pool crosses.

Midparent heterosis (*MPH*)

In both ME and GE, considerable variation in MPH for seed yield was found among the crosses within each

Table 3 Estimates of the predicted selection response $\Delta G(\alpha)$ and the predicted usefulness $U(\alpha)$ at selection intensities $\alpha = 20\%$ and $\alpha = 1\%$ for seed yield in $\mathrm{F}_{3:4}$ lines derived from 36 faba bean crosses and evaluated over three environments, averaged over the six crosses within each crossing group

Crossing group	$\alpha = 20\%$						$\alpha = 1\%$					
	San Biagio		Tadla		Hohenheim		San Biagio		Tadla		Hohenheim	
	$\Delta G(\alpha)$	$U(\alpha)$	$\Delta G(\alpha)$	$U(\alpha)$	$\Delta G(\alpha)$	$U(\alpha)$	$\Delta G(\alpha)$	$U(\alpha)$	$\Delta G(\alpha)$	$U(\alpha)$	$\Delta G(\alpha)$	$U(\alpha)$
Minor × Minor	0.45	1.61	1.07	6.7	3.89	24.0	0.85	2.00	2.00	7.5	7.42	27.5
Major × Major	0.81	4.01	0.47	9.3	3.84	26.5	1.54	4.74	0.89	9.6	7.32	29.3
Mediterranean × Mediterranean	0.83	5.83	2.39	16.8	4.20	15.8	1.58	6.40	4.56	18.2	8.01	18.9
Minor × Major	0.82	3.61	1.56	9.8	3.22	27.7	1.57	4.35	2.97	11.0	6.14	30.6
Minor × Mediterranean	0.84	4.74	2.41	11.9	3.40	21.1	1.59	5.50	4.59	13.4	6.48	24.1
Major × Mediterranean	0.78	5.19	3.29	11.8	3.36	23.0	1.48	5.90	6.26	13.3	6.39	26.1
Mean of intra-pool crosses	0.67	3.82	1.29	10.9	3.97	22.1	1.31	4.40	2.47	11.8	7.57	25.3
Mean of inter-pool crosses	0.81	4.51	2.27	11.2	3.33	23.9	1.55	5.25	3.36	12.6	6.34	26.9
Overall mean	0.74	4.16	1.76	11.1	3.63	23.0	1.43	4.83	4.33	12.2	6.92	26.1

crossing group (Table 4). Estimates of MPH were higher in GE than in ME for most of the intra- and inter-pool crosses. Mediterranean intra-pool crosses in the ME, and Minor × Major inter-pool crosses in the GE, had a higher mid-parent heterosis as compared to other groups of crosses. The average MPH for seed yield ranged from 4.7 g in Minor intra-pool crosses to 15.8 g in Mediterranean intra-pool crosses in ME and from 11.6 g in Mediterranean intra-pool crosses to 17.9 g in Minor × Major inter-pool crosses in the GE. A similar trend was observed in the MPH for plant height and seeds per plant (data not shown).

Absolute difference between the parental means ($|\mathrm{P}_1 - \mathrm{P}_2|$)

In all three environments, estimates of $|\mathrm{P}_1 - \mathrm{P}_2|$ for seed yield showed substantial variation among the six crosses in each group (Table 4). Likewise, estimates of $|\mathrm{P}_1 - \mathrm{P}_2|$ averaged across the six crosses showed a large variation among different crossing groups at Tadla and Hohenheim. Inter-pool crosses had a higher mean $|\mathrm{P}_1 - \mathrm{P}_2|$ for seed yield than the intra-pool crosses in all environments. For individual crosses, the highest estimates of $|\mathrm{P}_1 - \mathrm{P}_2|$ were obtained in Minor × Mediterranean inter-pool crosses at San Biagio and Hohenheim, and in Mediterranean intra-pool crosses at Tadla.

Correlation of population parameters with various predictors

Prediction of population mean

Correlations between $\bar{\mathrm{P}}$ and $\bar{\mathrm{F}}_{3:4}$ for seed yield in both intra- and inter-pool crosses were highly significant ($P < 0.01$) and positive at San Biagio and Hohenheim (Table 5). In contrast, the corresponding correlations at Tadla were nonsignificant (data not shown). For days to anthesis, plant height, and seeds per plant, the correlations between $\bar{\mathrm{P}}$ and $\bar{\mathrm{F}}_{3:4}$ were significantly positive at San Biagio in both groups of crosses. The means of $\mathrm{F}_{3:4}$ lines were also closely correlated with mid-parent values for days to anthesis in inter-pool crosses and for seeds per plant in both groups of crosses at Hohenheim.

Prediction of genetic variance

Neither $\widehat{\mathrm{GD}}$ nor D^2 showed any significant associations with $\hat{\sigma}_g^2$ for seed yield in either group of crosses at all three locations (Table 5). For other traits too, $\hat{\sigma}_g^2$ did not show any significant correlation with either measure of genetic distance ($\widehat{\mathrm{GD}}$ or D^2) except for days to anthesis in intra-pool crosses at San Biagio, where it had a significantly positive association with D^2. Correlations of $\hat{\sigma}_g^2$ with absolute MPH for seed yield and seeds per plant were positive in both groups of crosses at San Biagio and in inter-pool crosses at Hohenheim, but their magnitude was too small to be of practical use.

For seed yield and seeds per plant, the correlations of $\hat{\sigma}_g^2$ with $|\mathrm{P}_1 - \mathrm{P}_2|$ were positive but nonsignificant in both intra- and inter-pool crosses at San Biagio and Hohenheim (Table 5). Similar results were obtained for seed yield at Tadla (data not shown). Significantly positive correlations between $\hat{\sigma}_g^2$ and $|\mathrm{P}_1 - \mathrm{P}_2|$ for days to anthesis were found in inter-pool crosses at San Biagio. All other correlations of $\hat{\sigma}_g^2$ with the various predictors were non-significant and low.

Prediction of usefulness

The predicted usefulness (U) for seed yield had in most cases highly significant and positive correlations with the means of the parents ($\bar{\mathrm{P}}$) and $\mathrm{F}_{3:4}$ lines ($\bar{\mathrm{F}}_{3:4}$)

Table 4 Estimates of the genetic distance between parents measured by RAPD markers (GD) and multivariate analysis of 53 morphological traits (D^2), the absolute difference between the parental means ($|P_1 - P_2|$) in three environments [San Biagio (SBI), Tadla (TAD), and Hohenheim (HOH)], and estimates of the absolute mid-parent heterosis across seven Mediterranean (MPH_{ME}) and two German environments (MPH_{GE}) for seed yield in 36 faba bean crosses

Crossing groups crosses	GD	D^2	(g plant^{-1})				
			$\lvert P_1 - P_2\rvert$			MPH_{ME}	MPH_{GE}
			SBI	TAD	HOH		
Minor × Minor							
K25 × N36	0.52	38.2	0.74	0.09	0.83	5.1	8.6
K25 × H20S	0.53	76.9	1.21	0.21	8.63	3.1	13.3
K25 × SCI	0.49	27.8	0.51	0.57	2.43	4.6	15.3
KT42 × N36	0.49	46.0	0.69	2.83	13.34	5.8	15.3
KT42 × SCI	0.52	47.6	0.92	3.49	11.74	3.2	18.6
14C × SCI	0.53	36.0	2.21	4.39	2.93	6.1	16.1
Mean	0.51	45.4	1.05	1.93	6.62	4.7	14.5
Major × Major							
Fel × CAm	0.43	62.4	1.92	3.56	1.77	5.9	15.8
Fel × Hed	0.46	71.3	1.62	3.57	1.95	10.8	12.2
Fel × CEx	0.38	85.7	2.25	0.12	4.24	8.1	19.5
Min × CAm	0.43	67.8	0.26	2.88	2.34	4.3	5.4
Min × Hed	0.46	60.2	0.04	4.25	2.16	3.9	9.5
Min × CEx	0.46	58.3	0.59	0.56	0.13	10.2	13.4
Mean	0.44	67.6	1.11	2.49	2.10	7.2	12.6
Mediterranean × Mediterranean							
Giz × 98T	0.52	67.2	2.45	0.49	6.91	17.9	16.9
Giz × 135E	0.51	31.7	2.26	1.71	1.68	17.2	10.6
Giz × 13S	0.50	44.6	1.73	3.82	1.96	13.7	9.6
129T × Reb	0.48	70.3	2.06	31.24	3.02	14.3	11.6
129T × 34M	0.53	57.1	2.25	29.11	4.17	13.3	9.6
129T × 135E	0.50	49.6	0.42	22.58	4.13	18.5	11.1
Mean	0.51	53.4	1.86	14.82	3.64	15.8	11.6
Minor × Major							
K25 × CAm	0.49	166.7	3.13	0.80	1.27	8.2	15.3
KT42 × Hed	0.47	148.1	1.40	5.01	12.72	3.9	13.8
KT42 × CEx	0.49	135.1	2.03	1.32	10.43	10.9	17.9
14C × CEx	0.51	148.8	0.74	0.42	4.24	11.8	20.0
H20S × Row	0.56	82.0	0.32	8.06	8.24	2.7	18.9
SCI × Min	0.50	127.4	2.36	4.25	1.18	6.4	21.4
Mean	0.50	134.7	1.66	3.31	6.35	7.3	17.9
Minor × Mediterranean							
K25 × 135E	0.52	139.7	3.90	11.36	8.46	9.7	16.5
KT42 × 135E	0.55	141.4	2.47	8.44	22.63	13.2	14.9
N36 × 129T	0.52	167.3	2.74	33.85	5.16	12.4	8.0
H20S × Giz	0.53	47.3	4.95	9.86	1.85	9.5	19.4
H20S × Pel	0.57	69.0	2.67	4.70	14.01	7.9	18.0
SCI × Giz	0.58	173.8	5.65	10.22	9.21	16.8	11.2
Mean	0.55	123.1	3.73	13.07	10.22	11.6	14.6
Major × Mediterranean							
Fel × Reb	0.50	120.5	4.33	1.66	6.85	20.4	19.9
Fel × 135E	0.45	99.8	2.69	7.00	7.96	19.6	20.7
Min × 98T	0.48	87.9	0.84	5.48	3.48	11.8	7.6
Row × Reb	0.49	132.7	4.01	5.15	6.96	17.1	12.5
CAm × 129T	0.50	64.0	0.35	33.14	5.60	9.6	5.8
Hed × Pel	0.50	122.8	1.05	3.44	3.93	10.5	18.7
Mean	0.49	104.6	2.21	9.31	5.80	14.9	14.2
Means of intra-pool crosses	0.48	55.5	1.34	6.41	4.13	9.2	12.0
Means of inter-pool crosses	0.51	120.8	2.53	8.56	8.10	11.2	15.6
Overall mean	0.49	88.1	1.94	7.49	6.11	10.2	14.2

as well as with $\hat{\sigma}_g^2$ and ΔG at both low ($\alpha = 20\%$) and high ($\alpha = 1\%$) selection intensities in all three environments (Table 5, data for Tadla not shown). Among all measures, U was most closely associated with $\bar{F}_{3:4}$ especially under low selection intensity ($\alpha = 20\%$). Correlations of U with ΔG and $\hat{\sigma}_g^2$ were of a similar magnitude and comparable to those for $\bar{F}_{3:4}$ under high selection intensity.

Table 5 Correlation coefficients r(X, Y) between (1) means of the parents ($\bar{P}$) and $F_{3:4}$ lines ($\bar{F}_{3:4}$), (2) genetic variance ($\hat{\sigma}_g^2$) and two measures of genetic distance between parents (GD, D^2), absolute difference between the parental means ($|P_1 - P_2|$) and absolute mid-parent heterosis (MPH) for seed yield, days to anthesis, plant height, and seeds per plant, and (3) predicted usefulness (U) and means of parents ($\bar{P}$), $F_{3:4}$ lines ($\bar{F}_{3:4}$), $\hat{\sigma}_g^2$, and predicted selection response (ΔG) in two environments (San Biagio and Hohenheim)

Variables		San Biagio		Hohenheim	
X	Y	Intra-pool	Inter-pool	Intra-pool	Inter-pool
		Seed yield (g plant^{-1})			
$\bar{P}$	$\bar{F}_{3:4}$	0.63*	0.70*	0.64*	0.96**
GD	$\hat{\sigma}_g^2$	0.04	−0.34	−0.12	0.03
D^2	$\hat{\sigma}_g^2$	−0.35	−0.03	0.00	0.42
$\|P_1 - P_2\|$	$\hat{\sigma}_g^2$	0.36	0.44	0.25	0.37
MPH	$\hat{\sigma}_g^2$	0.37	0.24	−0.08	0.49
$U(\alpha = 20\%)$	$\bar{P}$	0.71**	0.56*	0.65*	0.90**
$U(\alpha = 20\%)$	$\bar{F}_{3:4}$	0.94**	0.91**	0.94**	0.95**
$U(\alpha = 20\%)$	$\hat{\sigma}_g^2$	0.55*	0.35	0.67**	0.44
$U(\alpha = 20\%)$	ΔG	0.49	0.21	0.76**	0.45
$U(\alpha = 1\%)$	$\bar{P}$	0.72**	0.33	0.53*	0.81**
$U(\alpha = 1\%)$	$\bar{F}_{3:4}$	0.82**	0.73**	0.87**	0.87**
$U(\alpha = 1\%)$	$\hat{\sigma}_g^2$	0.71**	0.64*	0.86**	0.62*
$U(\alpha = 1\%)$	ΔG	0.75**	0.53*	0.77**	0.64*
		Days to anthesis (days)			
$\bar{P}$	$\bar{F}_{3:4}$	0.61*	0.80*	0.51	0.84**
GD	$\hat{\sigma}_g^2$	0.11	0.07	0.51	0.30
D^2	$\hat{\sigma}_g^2$	0.71*	0.58	−0.07	−0.11
$\|P_1 - P_2\|$	$\hat{\sigma}_g^2$	−0.08	0.68*	−0.08	0.22
MPH	$\hat{\sigma}_g^2$	−0.28	−0.27	0.06	−0.57
		Plant height (cm)			
$\bar{P}$	$\bar{F}_{3:4}$	0.79**	0.63*	−0.58	0.27
GD	$\hat{\sigma}_g^2$	0.58	−0.08	0.00	−0.08
D^2	$\hat{\sigma}_g^2$	−0.18	0.11	0.14	0.11
$\|P_1 - P_2\|$	$\hat{\sigma}_g^2$	−0.09	0.00	−0.06	0.20
MPH	$\hat{\sigma}_g^2$	0.03	−0.21	0.14	−0.42
		Seeds per plant (number)			
$\bar{P}$	$\bar{F}_{3:4}$	0.81**	0.87**	0.80**	0.81**
GD	$\hat{\sigma}_g^2$	−0.05	−0.42	0.06	−0.15
D^2	$\hat{\sigma}_g^2$	−0.49	0.04	−0.39	0.41
$\|P_1 - P_2\|$	$\hat{\sigma}_g^2$	0.50	0.55	0.03	0.23
MPH	$\hat{\sigma}_g^2$	0.41	0.24	−0.18	0.27

*,** Significant at the 0.05 and 0.01 probability levels, respectively

Discussion

The breeding potential of base populations in terms of the proportion of elite inbreds produced depends mainly on two parameters: the mean and the genetic variance. In recent studies with maize (Melchinger et al. 1998) and wheat (H. F. Utz 1998, personal communication), only the means of the base populations could be predicted from the means of their parental lines. The main goal of the present study was to assess both parameters in intra- and inter-pool crosses in faba beans, a partially allogamous crop, and to predict them from the means and genetic distances of the parent lines.

Comparison of usefulness, means, and genetic variance of different germplasm groups

In each environment, crosses between germplasm adapted to the target region had the highest predicted usefulness for seed yield, i.e. Mediterranean intra-pool crosses in ME, and both intra- and inter-pool crosses among Minor and Major germplasms in the GE (Table 5). On average, the predicted usefulness of intra-pool crosses was similar to that of inter-pool crosses in all three environments. Since the predicted usefulness is a function of μ and had very close association with $\bar{F}_{3:4}$, a similar trend was observed for the mean performance of the parents and $F_{3:4}$ lines. Inter-pool crosses showed, on average, a minor yield superiority over the intra-pool crosses for parents and $F_{3:4}$ lines in the ME and GE. This was also true for plant height and seeds per plant (Tables 1 and 2).

Similar to the mean performance and the predicted usefulness, the highest estimates of $\hat{\sigma}_g^2$ for seed yield among $F_{3:4}$ lines were observed in intra-pool crosses at San Biagio and Hohenheim (Table 1). This was unexpected because inter-pool crosses are wider crosses as evident from the high D^2 values, and therefore, should release a larger genetic variance than intra-pool crosses. However, the average $\hat{\sigma}_g^2$ in different crossing groups differed largely over environments. This indicates that genetic diversity alone cannot explain the differences in $\hat{\sigma}_g^2$ among different crossing groups and that adaptation is another major factor influencing the genetic variance released in a cross, because it affects the gene expression at QTLs controlling trait variation. Furthermore, in our study intra-pool crosses were also fairly wide crosses, because the parents originated from genetically distant populations as reflected by the high GD estimates within each germplasm pool.

Looking at the ample variation released in intra-pool crosses of adapted germplasm, it is questionable whether inter-pool crosses should be used for line development in faba beans. The estimates of the predicted usefulness of crosses indicated that crosses of adapted germplasm should be most promising in their respective environments. Moreover, inter-pool crosses involving Mediterranean germplasm are prone to lodging in the GE. Link et al. (1996) compared hybrid performance and heterosis of intra-pool vs inter-pool crosses among three germplasm groups of faba beans and arrived at similar conclusions for hybrid development.

Prediction of population means

In the absence of epistasis, the mean performance of $F_{3:4}$ lines derived by single-seed descent depends on the mean performance of the parents and dominance effects (Mather and Jinks 1982):

$$\mu_{F_{3:4}(P1 \times P2)} = \mu_{\bar{P}(P1 \times P2)} + d/8, \qquad (6)$$

where d is sum of dominance effects in the cross P1 × P2. Thus, unless there are very large dominance or epistatic effects, $\mu_{\bar{P}} = (\mu_{P1} + \mu_{P2})/2$ should be a good predictor of $\mu_{F_{3:4}(P1 \times P2)}$ and even more so for advanced selfing generations. Our results were in agreement with these theoretical expectations and indicated that the means of $F_{3:4}$ lines for all traits at San Biagio and for seed yield and seeds per plant at Hohenheim can be predicted reliably from the means of their parents (Table 5). However, correlations between $\bar{P}$ and $\bar{F}_{3:4}$ were non-significant at Tadla. This could be due to the relatively large standard errors associated with $\bar{P}$ and $\bar{F}_{3:4}$ as compared to the variation in these means because of the stressful climatic conditions at this location (heavy rainfall after planting and severe drought during flowering).

Prediction of genetic variance

In agreement with studies in oats (Moser and Lee 1994) and soybean (Kisha et al. 1997), neither $\widehat{GD}$ nor any other predictor could predict $\hat{\sigma}_g^2$ for seed yield among $F_{3:4}$ lines at different crosses. The explanation of this result requires some biometrical considerations. Suppose we want to investigate the correlation $r(X, Y)$ between two variables X and Y, each of which can only be measured with some error, i.e. $X^* = X + \varepsilon_X$ and $Y^* = Y + \varepsilon_Y$. Assuming that ε_X and ε_Y are stochastically independent from each other and from X and Y, we obtain the following correlation between X* and Y*:

$$r(X^*, Y^*) = r(X, Y) \cdot h_X \cdot h_Y, \qquad (7)$$

where $h_X^2 = \sigma_X^2/\sigma_{X^*}^2$, and $h_Y^2 = \sigma_Y^2/\sigma_{Y^*}^2$ are the repeatabilities of X* and Y*. Applied to our study, this shows that a low correlation between $\hat{\sigma}_g^2$ and a predictor $\hat{Y}$ can be attributed to the following reasons: (1) $\hat{\sigma}_g^2$ has a low repeatability due to its high standard error, (2) $\hat{Y}$ estimates Y with a large error and/or bias, and (3) the correlation $r(\sigma_g^2, Y)$ between the "true" values is low. This situation is similar to using phenotypic trait correlations as an indicator of genotypic trait correlations.

Considering the first reason, estimates of the standard error of $\hat{\sigma}_g^2$ for seed yield were larger than $\hat{\sigma}_g^2$ itself in most of the crosses at San Biagio and in some crosses at Tadla (data not shown). In order to reduce the standard error for $\hat{\sigma}_g^2$, a greater number (>100) of lines from each cross must be evaluated in larger plots with higher number (3–4) of replications. In this study, we evaluated 50 $F_{3:4}$ lines from each cross in two replications with a relatively small plot size, which particularly in the ME was not adequate to obtain sufficiently precise estimates of σ_g^2. Furthermore, competition between $F_{3:4}$ lines may affect the estimates of σ_g^2 in the various groups of crosses differently. On the other hand, testing of a greater number of lines in larger plots limits the number of crosses that can be evaluated to examine the predictive power of a predictor $\hat{Y}$.

Regarding the second reason, GD estimates calculated from RAPD markers may have a large error and/or bias on the following grounds. (1) The map position and, consequently, the genome coverage is generally unknown. Hence, important genome regions might not be represented adequately. (2) Bands at identical gel positions may not represent identical DNA fragments amplified, leading to a bias in the GD estimates (Link et al. 1995). (3) Mis-scoring or irreproducible bands are further sources of experimental error but, relative to the variation in GD estimates, they are only of secondary importance (Link et al. 1995).

Examining the third reason, for crosses between unrelated parents the correlation $r(\sigma_g^2, \mathrm{GD})$ depends on: (1) the linkage disequilibrium between the QTLs contributing to σ_g^2 and the marker loci used for estimating GD, and (2) the variation in the magnitude of gene effects at different QTLs. Using similar arguments as in previous investigations on the relationship between $\widehat{\mathrm{GD}}$ and MPH (Charcosset et al. 1991; Bernardo 1992), it can be shown that: (1) markers unlinked to QTLs, and (2) QTLs unlinked to markers, both reduce the correlation (Melchinger, unpublished results). Since the parent lines in this study originated from different germplasm pools, some linkage disequilibrium between QTLs and linked markers can be expected. However, as pointed out in an investigation on the correlation between $\widehat{\mathrm{GD}}$ and MPH (Charcosset and Essioux 1994), different linkage phases between QTLs and marker loci can exist in different germplasm groups, which will also reduce the correlation $r(\sigma_g^2, \mathrm{GD})$. Summarizing, the prospects to predict σ_g^2 reliably from molecular markers are low unless the position of QTLs affecting a given trait is known and closely linked polymorphic markers can be selected to calculate trait-specific GD estimates between the parents.

In crosses among related lines, the situation is different for two reasons. First, the expected GD and σ_g^2, which depends on the proportion of heterozygous QTLs, are a linear function of the co-ancestry coefficient f (Melchinger 1993). Owing to the dependence of both variables on f, a close association between them is expected. Second, the range in GD and σ_g^2 is usually much wider in crosses among related parents than in crosses among unrelated parents. This may well explain the poor correlations, $r(\hat{\sigma}_g^2, \widehat{GD})$, observed in this study as compared to other investigations (Bhatt 1973; Sarawat et al. 1994) involving crosses among related as well as unrelated lines. This is confirmed by the study of Moser and Lee (1994) in oats, in which a significant correlation between RFLP-based $\widehat{\mathrm{GD}}$ and $\hat{\sigma}_g^2$ dropped to a non-significant level when two crosses between closely related parents were excluded from the analysis.

Consistent with the results in oats (Moser and Lee 1994), D^2 in our study was also an unreliable predictor for $\hat{\sigma}_g^2$. This is most probably due to the fact that D^2 is a distance measure based on many quantitative and qualitative traits, whose expression is greatly modified by environmental factors. Since D^2 is not trait-specific but measures the overall diversity of parents in a given environment, it suffers from similar problems as $\widehat{\mathrm{GD}}$ based on RAPDs and does not adequately reflect the true genetic diversity at QTLs affecting σ_g^2 for a given trait.

Even though the correlations between MPH and $\hat{\sigma}_g^2$ for seed yield were non-significant, there was a clear trend that crosses with increased heterosis released a larger genetic variance in their progenies. In contrast to $\widehat{\mathrm{GD}}$ and D^2, MPH is both trait- as well as environment-specific and should be a good predictor of $\hat{\sigma}_g^2$ in the breeding of line cultivars if the degree of dominance is constant and greater than zero at all segregating QTLs affecting the trait expression (Melchinger, unpublished results). The results of a companion study (Schill et al. 1998) indicated that a wide variation exists in the degree of dominance among F_1 hybrids of the three germplasm groups. Despite the fact that heterosis for seed yield in faba beans amounts to about 50% (Link et al. 1996), it could also be possible that many QTLs show only additive gene action. Such QTLs would contribute to σ_g^2 but not to MPH. On the other hand, some QTLs may show dominance effects but the parental alleles may not differ in their additive effects and, consequently, would only contribute to MPH but not to σ_g^2. Under both the situations, $r(\sigma_g^2, \mathrm{MPH})$ will be reduced.

Correlations between $|\mathrm{P}_1 - \mathrm{P}_2|$ and $\hat{\sigma}_g^2$ for seed yield were positive at all three locations, but their estimates were too small to be of any of predictive value. A tight association between these two variables is expected only when all QTLs contributing to σ_g^2 are in coupling phase and have a similar effect. In contrast, QTLs in repulsion phase will contribute equally to σ_g^2 but their contribution to $|\mathrm{P}_1 - \mathrm{P}_2|$ will cancel each other (Melchinger et al. 1997). In the extreme case, $|\mathrm{P}_1 - \mathrm{P}_2|$ can be zero but σ_g^2 can be maximum if all QTLs for *per se* performance for a given trait in a cross $\mathrm{P}_1 \times \mathrm{P}_2$ are in a heterozygous state and P_1 carries the favorable alleles at half of these QTLs. A preponderance of coupling phase among QTLs can be expected in crosses between extreme parents with large values for $|\mathrm{P}_1 - \mathrm{P}_2|$. Such a situation very likely exists in crosses of Minor × Major germplasm for seed yield ($\bar{\mathrm{P}}_1 = 0.3$ g and $\bar{\mathrm{P}}_2 = 0.8$ g) and seed number per plant ($\bar{\mathrm{P}}_1 = 80$ and $\bar{\mathrm{P}}_2 = 25$), while for seed yield ($\bar{\mathrm{P}}_1 = 22$ g and $\bar{\mathrm{P}}_2 = 24$ g plant^{-1}) there should be a balance of coupling and repulsion phase linkages. In harmony with these theoretical considerations, a higher, though non-significant, correlation between $|\mathrm{P}_1 - \mathrm{P}_2|$ and $\hat{\sigma}_g^2$ was observed for seeds per plant than for other traits at San Biagio (Table 5).

In a recent study in European maize, Melchinger et al. (1998) obtained similar results for the prediction of testcross genetic variance. However, in their study the tester may have masked the contributions of heterozygous QTLs to σ_g^2. These authors also evaluated a multiple linear-regression model using estimates of both GD and $|\mathrm{P}_1 - \mathrm{P}_2|$ for predicting $\hat{\sigma}_g^2$. This yielded essentially the same result as the linear relationship with each trait. In our study, too, a multiple regression model did not improve the prediction of $\hat{\sigma}_g^2$.

Prediction of usefulness

Among the two components of usefulness, μ was the most important indicator for $U(\alpha)$, especially under low selection intensity ($\alpha = 20\%$), in all three environments. Under a high selection intensity ($\alpha = 1\%$), μ and ΔG were of equal importance for predicting $U(\alpha)$. However, more accurate estimates of σ_g^2 and h are required if ΔG is considered as a predictor of $U(\alpha)$. Obviously, these conclusions are limited to the genetic materials investigated in this study and may well be different in crosses between elite lines with a narrower genetic base. Another weakness of our study was that estimates of h^2 and σ_g^2 for Hohenheim were based on an evaluation of the materials in one environment. Multi-environment tests for a given target region would improve the accuracy of these estimates but also substantially increase the expenditures required for prediction and, thus, be prohibitive from a practical point of view, considering also the low multiplication coefficient in faba beans.

Conclusions

From the two components determining $U(\alpha)$ of a particular cross, only μ can be predicted reliably from the means of their parents, provided they have been evaluated intensively in multi-location trials over several years in the target environments. Using the mid-parent values of n lines, the mean performance of $n(n-1)/2$ possible crosses can be predicted and only those crosses with highest predicted means are produced and evaluated in advanced generations. This corresponds to the current practice of most breeders, which concentrate their efforts on crosses between elite parents. Our results clearly demonstrate the influence of adaptation to the target environment on the predicted usefulness and mean performance of the $F_{3:4}$ lines. Since crosses between adapted materials, i.e. Minor × Minor or Minor × Major in the GE and Mediterranean × Mediterranean crosses in the ME, released ample genetic variation and had a high mean performance in selfing progenies, there is currently little incentive for making wide crosses between adapted and exotic germplasm in faba bean breeding. Link et al. (1996) arrived at similar conclusions for the development of hybrid cultivars in faba beans. However, a prediction of the genetic variance among crosses was not possible from the properties of their parents and remains an open problem.

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