

Efficiency in the use of phosphorus, nitrogen and potassium in *topless* faba beans (*Vicia faba* L.) — variability and inheritance*

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Abstract

In a field experiment with *topless* faba beans, parental inbred lines and F₁ hybrids of a 7 × 7-diallel were evaluated for traits related to the P, N and K efficiency. In addition, the parental inbreds were cultivated in a pot experiment at two P levels (100 vs. 700 mg P per pot). Significant heterosis for grain yield, uptake and utilization efficiency of nutrients in the field experiment highlighted the enhancement of nutrient efficiency in the hybrids. Amongst both parental inbreds and hybrids, significant genotypic variation was found for nearly all recorded traits. In the diallel analysis, the GCA effects generally proved to be highly significant and in most cases considerably higher than the SCA effects. In the pot experiment, grain yield ranking of the parental lines at the high P level (= P700) was very similar to that in the field experiment, whereas at the low P level (= P100, = P deficiency) the ranking of the lines changed considerably. Correspondingly, the P level-line interaction was highly significant. High tolerance towards P deficiency was found for those two parental inbreds derived from cultivars bred under Syrian conditions. At the high P supply, P efficiency was more favoured by a high P uptake, but at P deficiency by a high internal P utilization.

Key words: *Vicia faba* — diallel analysis — inheritance — nitrogen — phosphorus — potassium — nutrient efficiency

Today, the input of mineral fertilizer, particularly of nitrogen and phosphorus, is often reduced for economical as well as ecological reasons. Conditioning factors are unfavourable output/input relationships due to increasing input costs and reduced market prices and environmental contamination problems, as indicated by considerable nitrate and phosphate levels in the ground and surface water, respectively. In order to at least maintain high yield and product quality, a considerable number of biotic and abiotic resources is available, suited to improving the supply and uptake of soil-borne nutrients and applied fertilizers (review: Sattelmacher et al. 1994). The more important among these resources are:

- Diversification of crop rotations by species with an improved ability to mobilize nutrients in the rhizosphere (e.g. lupin, red and white clover; Gerke 1995) as well as nitrogen fixing legumes (e.g. faba bean and dry pea; Köpcke 1987);
- Use of VA-mycorrhiza and of non-symbiotic nitrogen fixing bacteria (see Marschner 1995);
- Agronomic as well as agrochemical measures to keep nitro-

gen in the top soil by cultivation of catch crops and use of nitrification inhibitors, and;

- Last but not least, cultivation of cultivars exhibiting a high efficiency in biological use of fertilizers and soil nutrients.

In the near future, therefore, breeding and cultivation of highly nutrient-efficient cultivars are not only of special interest for the least developed countries, which frequently are characterized by high percentages of soils with low nutrient supply and/or unfavourable nutrient dynamics (Vlek and Koch 1992), but will also become increasingly important for highly developed countries. Genetic variation for nutrient efficiency has been reported within crop species, but extensive studies on this variability and the inheritance of traits related to nutrient efficiency have been conducted particularly for cereals, oil and fodder crops (Clark and Duncan 1991, Sattelmacher et al. 1994). In most temperate grain legumes, little data have been published on this topic except for the traits directly related to the symbiotic nitrogen fixation.

In the present investigation, faba beans were used (1) to study the variability and inheritance of traits of the phosphorus (P), nitrogen (N) and potassium (K) uptake and utilization efficiency, (2) to evaluate the effect of a reduced P supply on traits of the P and N efficiency, and (3) to identify genotypes with an improved tolerance to P deficiency.

Materials and Methods

Genotypes: Parents and F₁ hybrids of a 7 × 7-diallel with faba beans were grown in 1993. All parental lines were of the *topless* growth type. Each line consisted of one S₁ single plant progeny taken at random from the cultivars 'Piccolo' (D), 'Ticol' (GB) and 'Tina' (D) as well as from breeding strains derived from 'Alfred' × *ü*₁ (D), 'Minica' × *ü*₁ (D), D84233-6-1 (Syr) and Flip87-126FB (Syr). The cultivars were bred in Germany (D), Great Britain (GB) and Syria (Syr), respectively. They differ considerably in phenology, yield structure and yield level. In comparison with the indeterminated, open-pollinated cultivar 'Alfred', the respective performance means of which are given in parentheses, the following ranges were observed by Stelling (1996) for the performance of the seven parental inbreds: -2 to +5 days for onset of flowering (162), -12 to -4 days for date of maturity (240), -62 to -23 cm for plant length (112), ± 0.0 to +1.7 for podded lateral stems/plant (0.6), -6.5 to -3.7 for podded nodes/main stem, -0.7 to +0.5 for seeds/pod (3.0), -243 to +151 g for 1000-grain weight (572), and -22.7 to -12.0 g for grain yield/plant (36.8). Hybrids were produced by hand crossing in bee-proof isolation cages. Bulk seed of the generations S₂ and S₃ was used for the crossing and that of the generations S₃ and S₄ for the sowing in the field and pot experiments.

*Dedicated to Prof. Dr. G. MICHAEL, Stuttgart-Hohenheim, on the occasion of his 85th birthday.

Field experiment: Parents ($n = 7$) and F_1 hybrids ($n = 21$) of the 7×7 -diallel were grown near Göttingen on a highly fertile loam soil with high P and K status (23 mg $P_2O_5/100$ g soil and 22 mg $K_2O/100$ g soil measured by calcium lactate acetate extraction (CAL-P and CAL-K)). The experimental layout was a completely randomized block design with three replicates. Plots consisted of one single row, 1.50 m in length, sown with 12 seeds. Spacing between rows was 0.33 m. In order to reduce border effects and neighbouring effects between adjacent entries, the short-strawed, highly lodging-resistant faba bean cultivar 'Mythos' was sown every second row and at both front sides cross to the entry rows. A trickle irrigation was installed to secure a sufficient water supply during the generative phase. At maturity, all plants of each entry row were harvested.

Pot experiment: For the pot experiment, only the seven parental lines were used. For cultivation, Mitscherlich pots, 20 cm in diameter and 20 cm in depth, were filled with a 50:50 mixture of quartz sand and a loessloam subsoil known for its very low P and N free status (Luvisol from Ellichhausen near Göttingen; pH ($CaCl_2$) 7.7 and < 1 mg $P_2O_5/100$ g soil (CAL-P)). Each pot was fertilized with 1.8 g K (K_2SO_4), 0.3 g Mg ($MgSO_4 \cdot 4H_2O$) and a micro-nutrient solution after Schropp (1951). No nitrogen was applied. To ensure inoculation of plants with rhizobia, small amounts (10 g/pot) of soil from the nursery of the field experiment were mixed with the pot substrate. The plants were grown at two diverse P levels: half of the pots got 100 mg P ($NaH_2PO_4 \cdot 2H_2O$), the others 700 mg P. In each pot, four plants were cultivated at 70% of maximum water capacity until maturity. The plants grew in an open-air hall and were transported into the adjacent greenhouse at night. Experimental layout was a completely randomized design with four replicates. All plants of each pot were harvested at maturity.

Characters: On the basis of rows in the field experiment and of pots in the pot experiment, the dry matter yields of grains and straw (in g/plant) and their appropriate P and N content (in percentage dry matter) were recorded. In the field experiment, in addition, the K content (in percentage dry matter) was measured. From these records, the grain N yield (in mg/plant), shoot P, N, and K uptake (in mg/plant), P, N, and K utilization efficiency (in mg dry matter grain/mg nutrient in the total shoot dry matter), and P, N, and K harvest index (grain nutrient yield/shoot nutrient uptake; in percentage) were calculated.

P, N, and K measurement: Dried (24 h at 105°C) and ground plant material was digested with HNO_3 in teflon bombs at 180°C. The P content was measured according to Kitson and Mellon (1944) and the K content directly by a flame photometer. N content was determined by dry digestion in a closed system and the thermal conductivity was measured with the Nitrogen Analysator FP-228 from Leco Corporation (St. Joseph, MI, USA).

Statistical analysis: For data analysis, conventional analysis of variance was used. The diallel analysis and calculation of estimates of general combining ability (= GCA) were performed according to the fixed-effects model described by Griffing (1956). If the F -test revealed significance, L.S.D._{5%} values were calculated.

Results

In the field experiment, the average grain yield of the F_1 hybrids was 51% higher than that of their parental inbreds. For traits highly related with grain yield (i.e. P, N, and K uptake, and grain N yield; $r_p > 0.95^{**}$) the heterosis level was only slightly lower, whereas small negative heterosis values were observed for the different nutrient contents and small positive ones for the P, N and K utilization, as well as for the P and N harvest index (Table 1). For most traits, significant genotypic variation was found within both generations of the diallel (Tables 1 and 2). However, with the exception of grain yield and its highly

related characters (see above), genotypic variation proved to be relatively small (Table 1).

The analysis of variance for the P, N, and K efficiency traits of the diallel is shown in Table 2. In general, the variation due to general combining ability (GCA) was highly significant and in most cases considerably larger than that due to the rarely significant values for the specific combining ability (SCA). GCA effects of the parental lines are given in Table 3. Many favourable GCA effects were found for 'Tina'/4 — in favour of a high grain and grain N yield, a high P, N, and K uptake, a high P and K utilization, high N harvest index but low grain P, grain K, and straw N content. Nearly the opposite is true for Flip87-126FB/3 frequently showing the most unfavourable values, which in part is also true for the lines 'Alfred' \times $t_1/1$ and 'Minica' \times $t_1/1$. For most traits, GCA effects proved at least moderately correlated with the parental performance *per se* (Table 3).

In the pot experiment, grain yield and its highly related traits (see above) were heavily reduced at the low P level. As a result of the low grain P content (-34%), the P utilization at P100 was significantly higher (+38%) than at P700 (Table 4 and Fig. 1). However, as indicated by the highly significant P level-line interaction (Table 4), the lines differed in their sensitivity towards P deficiency. The smallest grain yield reduction, i.e. highest tolerance towards P deficiency, was observed for Flip87-126FB/3 (-40%) and D84633-6-1/2 (-49%) and the highest grain yield reduction, i.e. lowest tolerance, for 'Tina'/4 (-63%). As a consequence, Flip87-126FB/3 reached rank 1 at P100 compared to rank 5 at P700 (Fig. 1a). The higher grain yield of Flip87-126FB/3 and D84633-6-1/2 at P100 seemed to result more from the improved P utilization than the less decreased P uptake (Fig. 1b,c). With the exception of N uptake and grain N yield, the other N related traits were not or only slightly modified (Table 4).

Discussion

Genotypic variation for macro-nutrient efficiency traits at high P supply

For the most complex traits of the P, N, and K efficiency, i.e. grain yield as well as P, N, and K uptake, a considerable genotypic range was found within both generations of the diallel. F_1 hybrids, however, outyielded their parental lines significantly. Midparental heterosis values of 51, 36, 40 and 39%, respectively, were observed for the above mentioned characters (Table 1). For grain yield, heterosis of similar magnitude has been reported in indeterminate faba beans (see Link et al. 1994, Stelling et al. 1994). Yield advantage of the hybrids resulted from both a higher uptake (+36 to +40%) and a higher utilization of macro-nutrients (+7 to +11%; Table 1), thus implementing the improved nutrient uptake and utilization efficiency of the hybrids when the supply of P is high. This was especially true for the hybrids of line 'Tina'/4, as indicated by the highest GCA effects for grain yield as well as for P, N, and K uptake (Table 3). Obviously, the ability of these hybrids to acquire P, N, and K from the soil and/or to fix N from the atmosphere was exceptionally improved. Considerably lower heterosis values were observed for the component traits P, N, and K harvest index and even negative ones were found for the grain P, grain N, and grain K content (Table 1). Smaller grain nutrient contents of the hybrids are favoured by their considerably increased accumulation of assimilates, giving rise to a dilution of nutrient concentration and thus indicating a negative

Table 1: Average performance and range of parental inbreds and F₁ hybrids of the 7 × 7-diallel for P, N, and K efficiency traits in the field experiment

Character	Parental inbreds			F ₁ hybrids			Relative hybrid performance
	Mean	Range	CV _g ¹	Mean	Range	CV _g ¹	
Grain yield (g/plant)	22.8	15.1–34.9	32	34.4	20.0–45.7	20	151**
Grain P content (%)	0.60	0.54–0.67	9	0.55	0.51–0.63	5	92**
P uptake (mg/plant)	162	108–247	31	221	149–297	18	136**
P utilization (mg/mg)	141	119–155	9	156	133–174	6	111**
P harvest index (%)	83.1	77.7–88.1	4	85.0	78.7–89.9	4	102**
Grain N content (%)	4.10	3.83–4.38	4	3.96	3.70–4.24	2	97**
N uptake (mg/plant)	1232	810–1880	33	1724	1030–2350	20	140**
N utilization (mg/mg)	18.6	17.7–20.0	3	20.0	18.6–20.9	2	108**
N harvest index (%)	76.1	71.1–80.1	4	79.0	72.1–82.8	3	104**
Grain N yield (mg/plant)	929	640–1350	28	1369	750–1810	21	147**
Straw N content (%)	1.55	1.38–1.72	4	1.42	1.20–1.69	8	92**
Grain K content (%)	1.32	1.15–1.49	7	1.24	1.12–1.34	5	94**
K uptake (mg/plant)	761	417–1329	37	1054	677–1396	18	139**
K utilization (mg/mg)	30.6	25.9–35.9	12	32.8	27.0–39.2	8	107**
K harvest index (%)	40.1	34.0–45.4	10	40.3	36.2–46.3	5	100

**Significant at P = 0.01

¹Coefficient of genotypic variation (in percentage): $CV_g = (\sigma_g/\bar{y}) \cdot 100$; σ_g^2 : genotypic component of varianceTable 2: Diallel analysis of the F₁ hybrids' performance for P, N, and K efficiency traits in the field experiment

Character	Block	Genotype	Mean squares		Error
			GCA	SCA	
Grain yield	248.9**	161.1**	464.3**	31.1	19.8
Grain P content	0.0055**	0.0027**	0.0079**	0.0005	0.0007
P uptake (× 10 ⁶)	0.0130**	0.0057**	0.0160**	0.0013	0.0008
P utilization	199.5*	347.0**	912.1**	104.9 ⁺	55.7
P harvest index	17.01*	31.20**	64.94**	16.74**	4.13
Grain N content	0.3527**	0.0603 ⁺	0.1350**	0.0283	0.0361
N uptake (× 10 ⁶)	0.5997**	0.4108**	1.1889**	0.0774	0.0612
N utilization	2.474*	1.112*	2.344**	0.584	0.579
N harvest index	53.98**	27.68**	57.76**	14.79*	7.02
Grain N yield (× 10 ⁶)	0.4890**	0.2874**	0.8133**	0.0621	0.0419
Straw N content	0.0421	0.0628**	0.1153**	0.0404 ⁺	0.0213
Grain K content	0.0302**	0.0124**	0.0341**	0.0031	0.0031
K uptake (× 10 ⁶)	0.1040*	0.1364**	0.3529**	0.0436	0.0272
K utilization	24.38*	25.95**	69.80**	7.16	5.89
K harvest index	34.84**	18.32**	36.38*	10.58	6.71
df	2	20	6	14	40

+, *, **Significant at P = 0.1, P = 0.05 and P = 0.01, respectively

relationship between grain yield and grain nutrient content. The mostly negative correlation coefficients between grain yield and grain P, grain N, and grain K content within both generations of the diallel (Table 5) are in agreement with the above trend and confirm earlier findings in other arable crops (e.g. Feil and Fossati 1995).

Although the causal agents of the observed heterosis are unknown, one may suppose that the highly improved P uptake of the hybrids is caused by either a higher P influx per root unit, an enlarged root surface (by length and/or diameter), or both. In *Lolium perenne*, for example, the higher P uptake of the hybrids (when compared with the parental inbreds) was definitely conditioned by a larger root system, whereas the P uptake per root unit was unchanged (W. Römer and J. Fahning, unpubl. data). A larger root system, however, means a higher demand for C and N metabolites which have to be provided by the shoot and rhizobia, respectively, as the result of an improved

symbiotic fixation of atmospheric nitrogen. In order to prove the above relationships for the present faba bean material and to get a deeper understanding of the specific effects of heterosis on P uptake and its interrelationship with the root morphology and symbiotic nitrogen fixation, more intensive morphological as well as physiological investigations are needed.

Genotypic variation for tolerance to P deficiency

At the low P level (= P100), the N uptake — being nearly equivalent to the amount of symbiotically fixed N, since a N free subsoil was used as growing substrate — and the grain yield were heavily reduced (Table 4). Present results therefore indirectly highlighted the importance of P for the symbiotic N fixation (cf. Graham and Rosas 1979). However, the significance of the line–P-level interaction and the observed changes in the ranking of the lines between P levels in the pot

Table 3: GCA effects of parental lines for P, N, and K efficiency traits and correlations with the performance in the field experiment *per se*

Character	Parental inbreds							GCA-effect vs. performance <i>per se</i>
	'Piccolo'/4	'Ticol'/3	'Tina'/4	'Alfred' × t ₁ /l	'Minica' × t ₁ /l	D84233-6-1/2	Flip 87-126 FB/3	
Grain yield (g/plant)	0.7	2.5*	10.9**	-4.7**	-4.3**	-0.7	-4.3**	0.74 ⁺
Grain P content (%)	-0.015*	-0.023**	-0.018**	0.010	-0.006	0.008	0.044**	0.88**
P uptake (mg/plant)	-7.0	12.2	64.6**	-33.6**	-29.1**	-0.8	-6.4	0.80*
P utilization (mg/mg)	8.1**	3.5	4.0*	3.1	-0.7	-2.1	-16.0**	0.65
P harvest index (%)	2.4**	-1.6**	-0.4	3.2**	-1.3*	0.2	-2.4**	0.39
Grain N content (%)	-0.04	-0.11*	0.11*	0.05	-0.13**	0.09	0.03	0.61
N uptake (mg/plant)	4.6	131.8*	551.7**	-254.7**	-253.0**	-24.6	-155.8*	0.77*
N utilization (mg/mg)	0.33	-0.03	-0.05	0.24	0.40*	-0.11	-0.77**	0.16
N harvest index (%)	0.5	-2.3**	2.1**	1.9**	-1.0	1.5*	-2.6**	0.00
Grain N yield (mg/plant)	13.2	54.3	472.4**	-175.0**	-210.8**	0.6	-154.8**	0.69*
Straw N content (%)	-0.09*	-0.04	-0.06	-0.07*	0.05	0.08*	0.14**	-0.14
Grain K content (%)	-0.014	0.001	-0.064**	-0.008	0.071**	-0.038**	0.053**	0.91**
K uptake (mg/plant)	39.6	143.2**	253.3**	-178.8**	-71.4	-110.0**	-75.9	0.78*
K utilization (mg/mg)	-0.64	-1.70**	2.15**	1.40*	-1.94**	3.01**	-2.28**	0.76*
K harvest index (%)	-1.1	-1.9**	0.5	1.5*	-0.2	2.4**	-1.1	0.64

⁺, *, ** Significant at P = 0.1, P = 0.05 and P = 0.01, respectively

Table 4: Analysis of variance of the inbred lines' performance in the pot experiment and the average effect of P deficiency on several P and N efficiency traits

Character	P level	Line	Mean squares		Average effect of P deficiency (%) ¹
			P level × line	Error	
Grain yield	341.9**	10.2**	4.8**	0.6	-57
Grain P content	0.3024**	0.0287**	0.0134**	0.0037	-34
P uptake (× 10 ⁶)	0.01396**	0.00018**	0.00009*	0.00003	-69
P utilization (× 10 ²)	802.4**	69.4**	30.3*	9.4	38
P harvest index	574.3*	357.5**	63.0**	13.8	-8
Grain N content	0.0000	1.6207**	0.1206	0.0969	0
N uptake (× 10 ⁶)	1.0990**	0.0174**	0.0080*	0.0027	-54
N utilization	21.94 ⁺	8.37**	4.52 ⁺	2.03	-8
N harvest index	448.4*	200.1**	51.7**	15.2	-8
Grain N yield (× 10 ⁶)	0.6791**	0.0118**	0.0074**	0.0019	-57
Straw N content	0.0605	0.0596**	0.0514*	0.0180	5
df	1	6	6	42	

⁺, *, ** Significant at P = 0.1, P = 0.05 and P = 0.01, respectively

¹ Calculated from $[(\bar{y}_{P100} - \bar{y}_{P700}) / \bar{y}_{P700}] \cdot 100$

experiment (Table 4 and Fig. 1) also indicate that genotypic differences do exist in the tolerance to P deficiency and the efficient use of a high P supply, respectively.

The present evaluation data are based on pot trials. Growing conditions in the Mitscherlich pots used differ considerably from field conditions, particularly for the root system. Nevertheless, a high, positive rank correlation ($r_s = 0.96^{**}$) was found between the average grain yield measured by Stelling (1996) over 2 years and four sowing dates in the field and that observed at the high P level in the pot trial (= P700; Fig. 1d). Thus, yield formation in the pot trial seemed to be similar to that in the field and an extrapolation of the present results to field conditions appears to be justified.

'Tina'/4 being highly responsive to increasing P availability represents a high-input genotype, whereas Flip87-126FB/3 can be characterized as a low-input genotype being far less responsive to increasing P supply than 'Tina'/4 and maintaining a relatively high yield level under conditions of very low P availability (i.e. P deficiency). Flip87-126FB/3 climbed from rank 5

at P700 to rank 1 at P100 and here even surpassed 'Tina'/4 (Fig. 1a). The present results therefore confirmed earlier findings (cf. Vose 1983, Sattelmacher et al. 1994) that the best performing genotype(s) under high fertilizer supply do not necessarily perform best under conditions where yields are limited by insufficient supply of nutrients and vice versa. The better P use efficiency at P100 of Flip87-126FB/3 predominantly resulted from the heavily increased P utilization within the plant. A similar reaction, but at a lower performance level, was observed for D84223-6-1/2 (Fig. 1a,c). Both lines were derived from breeding strains bred at the International Center of Agricultural Research in the Dry Areas (ICARDA) in Syria, where soils are often deficient in available P. Both breeding strains seem to be well adapted to low P availability and cultivation of the breeding materials under the above circumstances had obviously favoured the selection of genotypes with a high internal utilization efficiency.

The results of the pot experiment (Fig. 1) lead to assume that high- and low-input faba bean genotypes follow different

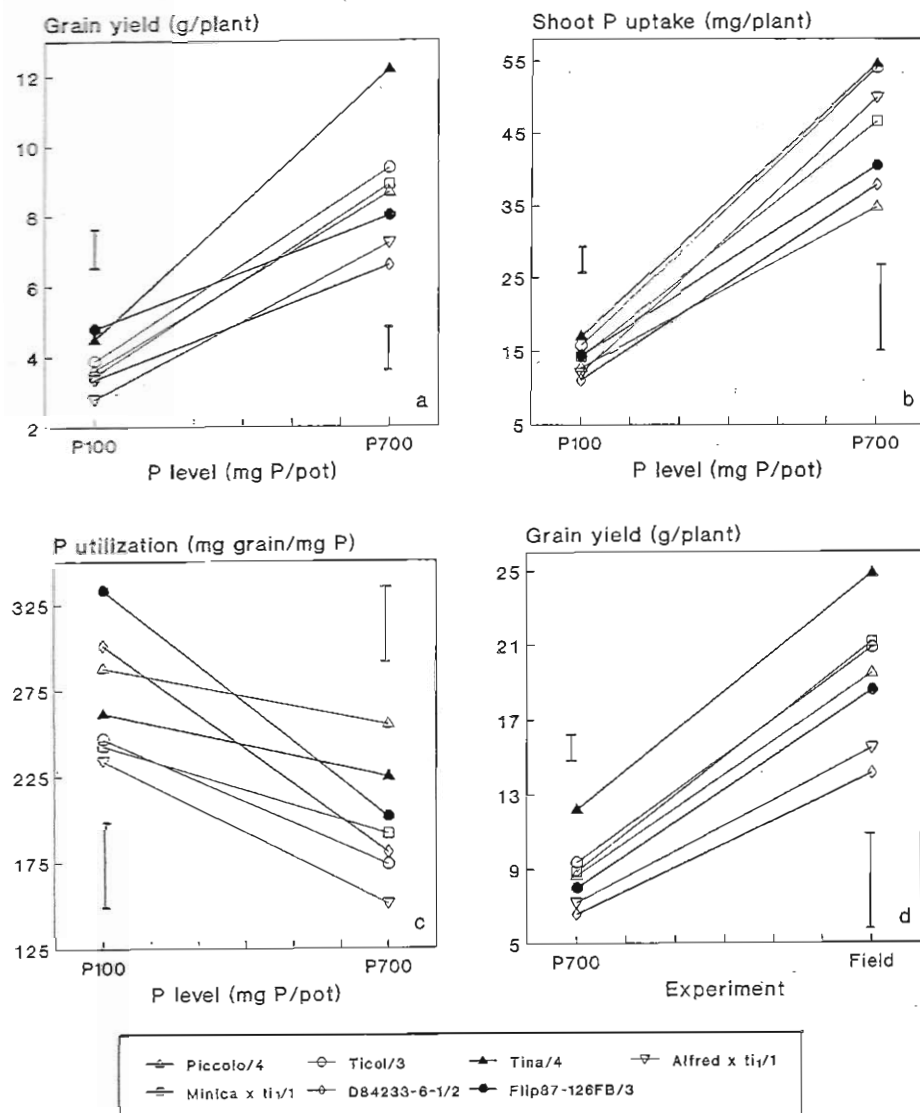


Fig. 1: Effect of the P fertilizer supply on grain yield (a), shoot P uptake (b) and P utilization (c) of the seven faba bean inbred lines in the pot experiment. In addition, in (d) grain yield at P700 and in the field experiment averaged over two years and four sowing dates (taken from Stelling 1996) are compared. Vertical bars indicate L.S.D._{5%} for lines at the correspondent P level

Table 5: Phenotypic correlation coefficients between grain nutrient content and grain yield within the parental and F₁ generation of the 7 × 7-diallel in the field experiment

Character	Grain yield	
	P	F ₁
Grain P content	-0.53	-0.53*
Grain N content	-0.73	0.39 ⁺
Grain K content	-0.42	-0.60**

⁺, *, **Significant at P = 0.1, P = 0.05 and P = 0.01, respectively

efficiency strategies. At high P supply, increments in grain yield are more easily achieved by an increased P uptake than by an improved internal P utilization. Under growing conditions of nutrient deficiency, the P uptake can hardly be increased, so that the internal P utilization gets the higher priority. In other crops, however, adaptation reactions are known which favour the P uptake even under conditions of P deficiency, particularly by modifications of root morphology (e.g. in wheat cultivars; Römer et al. 1989) and/or an increase of P mobilization by biochemical means (e.g. secretion of root exudates (citric acid etc.) in some leguminous species; Gerke 1995). An evaluation

of further germplasm accessions of faba beans derived from regions with P deficiency may be worthwhile to prove whether similar adaptations are also present in faba beans.

Breeding for improved nutrient use efficiency

The considerably different ranking of the lines between the two diverse P levels in the pot experiment (Fig. 1) indicates that the choice of selection environment may substantially determine the type of nutrient efficiency selected for: high-input efficient genotypes at location(s) with high nutrient availability and low-input efficient, i.e. deficiency tolerant genotypes at location(s) with low nutrient availability.

In Table 6, estimates of broad sense heritability for all the nutrient efficiency traits recorded in the field experiment at high P availability are given. Nearly all traits proved to be at least moderately heritable which is in agreement with results in other crops reviewed by Clark and Duncan (1991). The large variation due to GCA (Table 2) indicates that the genotypic differences observed for traits of the P, N, and K efficiency in the field experiment were predominantly determined by additive gene effects and therefore exploitable in any type of cultivar, i.e. lineal, synthetic as well as hybrid cultivars. In the long term,

Table 6: Estimates of broad sense heritability calculated on basis of the F₁ hybrids' performance in the field experiment

Character	Heritability (h _b ²)
Grain yield	0.76
Grain P content	0.69
P uptake	0.72
P utilization	0.69
P harvest index	0.72
Grain N content	0.29
N uptake	0.71
N utilization	0.29
N harvest index	0.54
Grain N yield	0.72
Straw N content	0.43
Grain K content	0.58
K uptake	0.63
K utilization	0.60
K harvest index	0.41

however, and as soon as the prerequisites for a commercial hybrid seed production are available (see Duc et al. 1992, Ederer and Link 1995), the breeding of hybrid cultivars will allow the full exploitation of heterosis (Ebmeyer and Stelling 1994, Stelling et al. 1994) also for traits related to nutrient efficiency. Then hybrids will become the most attractive type of cultivar, for which the line 'Tina'/4 will be a most preferable hybrid parent as indicated by its high GCA effects for grain yield and uptake of P, N, and K (Table 3).

In the present study, the F₁ hybrids were not evaluated in the pot experiment. Therefore, further investigations are required (1) to check whether the relatively high superiority of the F₁ hybrids holds true also under P deficient growing conditions, (2) to estimate the heritability of nutrient efficiency traits at low P availability, and (3) to examine the inheritance of the observed P deficiency tolerance of lines Flip87-126FB and D84223-6-1/2.

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