



Influence of genotype on phosphate uptake and utilization efficiencies in spring barley

W. Römer *, H. Schenk

Institut für Agrikulturchemie, Georg-August-Universität, von Siebold-Str. 6, D-37075 Göttingen, Germany

Accepted 30 September 1997

Abstract

To investigate the genetic variation of phosphate (P) uptake and P utilization efficiency, 24 high-yielding spring barley cultivars were grown in two pot experiments on a loess loam-sand mixture. In the first experiment, the plants grew until maturity under P stress (50% of the maximum yield), and in the second experiment, the plants grew until the stage of tillering (DC 25) at a low or at a high P supply.

At maturity, the range between cultivars with the highest and the lowest values were 30% for total dm yield (grain and straw), 28% for grain yield, 24% for P uptake efficiency (P in grain and straw), 26% for P concentration in grains and 24% for P utilization efficiency quotient PEQ (g dm grain per mg P in shoots) (mean of all cultivars = 100%). Grain yield was correlated with P uptake per plant, $r=0.71^{***}$, and with PEQ, $r=0.60^{**}$. Between P uptake and PEQ, there was only a weak relationship ($r=-0.14$). Therefore, a combination of high uptake efficiency and high PEQ in a cultivar may be possible.

At growth stage DC 25, the cultivars showed a significant variability in shoot biomass, P concentration, P removal, P influx, activity of acid phosphatases (P_{ac}) and root length. The ranking of the cultivars, however, was very different at the two P levels, but the root-length and the P_{ac} activity were more influenced by genotype than by the P supply.

As the relationships between grain yield, P removal, PEQ and the characters of the young plants cultivated under P stress were very weak ($r<0.43$), selection for P efficiency at the stage of tillering cannot be recommended. © 1998 Elsevier Science B.V.

Keywords: Barley cultivars; Phosphate nutrition; Phosphate influx; Phosphate efficiency; Acid phosphatase; Root length

1. Introduction

In this century, improved soil fertility management and plant breeding have been very successful in increasing grain yield (Feil, 1990a,b). However, the selection in the last 30 years has been conducted at a high nutrient level (N, P, K) in soils. From

this, it may be assumed that the high nutrient requirement of high yielding cultivars is associated with lower uptake and/or utilization efficiencies (e.g. amount of grain per kg N or P absorbed by plants). With changing ecological and economic conditions, nutrient efficiency may become of increasing importance as an objective in plant breeding. Currently, it is being discussed in the European Union (EU) whether extensification should be practised on the total arable land or

* Corresponding author.

Abbreviations: DC, decimal code, dm, dry matter

only in regions with lower cropping capacity. Consequently, the nutrient status of soil (including its phosphorus status) could differ widely in the future. This raises two questions. Are high-yielding modern cultivars, even under conditions of low nutrient supply, superior in yield to older cultivars or land races with a lower yield potential? How consistent is the ranking of different cultivars for yield and/or nutrient efficiency at a low in comparison to a high nutrient supply (e.g. phosphorus content of soil)?

Furthermore, phosphate efficiency is of special interest for developing countries with soils with unfavourable phosphate dynamics (Sanchez, 1976; Pagel et al., 1982). Nitrogen is also of central importance because it is often the most limiting factor in crop production (Yau and Thurling, 1987; El Bassam, 1989; Feil, 1992; Bänzinger et al., 1992; Sattelmacher et al., 1994). For phosphate, efforts are being made to select genotypes with a low P demand (Horst and Wiesler, 1986; Helal, 1990; Thung, 1990). Here, the P uptake efficiency characterized by P uptake per plant or unit ground area and the utilization efficiency, e.g. for cereals the amount of grain per unit of P taken up, defined as the phosphate efficiency quotient PEQ must be considered in breeding programmes. There are two ways of expressing the PEQ: PEQ refers either to the total dry matter [P(dm)EQ] or only to the grain dry matter (PEQ).

In the work reported in this paper, the variability of P uptake and utilization efficiency of modern high-yielding spring barley cultivars at low P supply were investigated. It is well known that with a low P supply, there are significant relations between root length and P uptake (Römer and Schilling, 1986) and between the activity of acid phosphatases of shoots and P status of shoots (Römer et al., 1995). Therefore, we also investigated whether plant characters including P concentration in the biomass, P uptake, root length and activity of acid phosphatases in the shoots vary with cultivar. Such plant characters could be used in the selection of P-efficient cultivars. For this purpose, 24 cultivars of spring barley were cultivated in pots under low and high P supply until the stage of tillering (DC 25, Zatoks et al., 1974) and under low P supply until maturity. Various

plant characters were studied to determine their significance as selection criteria of P efficiency in the early stage of development.

2. Material and methods

2.1. Cultivars used

We investigated 24 cultivars registered by the Bundessortenamt (BSA) between 1975 and 1989. The cultivar spectrum included malting barley as well as feed barley. The yield potential assessment from the BSA ranged from medium to high. The cultivars originated from seven European countries. The cultivars Golf and Cerise are closely related. Six cultivars (Alexis, Amazone, Berolina, Comtesse, Rumba, Toga) contain the cultivar Trumpf in different proportions in their pedigree (Baumer and Göppel, 1990).

2.2. Cultivation of plants to maturity

The plants were cultivated in white enamel pots (20 cm in diameter, 20 cm deep). The pots were filled with a mixture (3.5:3.5 kg) of quartz sand and a loess subsoil [Luvisol from Elliehhausen near Göttingen: sand 5%, silt 85%, clay 10%, pH (CaCl₂): 7.3]. This soil had a low P content. After extraction with calcium–acetate–lactate (CAL) (Schüller, 1969), less than 10 mg P₂O₅ kg⁻¹ soil were found. Each pot was fertilized with 1.5 g N as NH₄NO₃ and Ca(NO₃)₂, 1.8 g K as K₂SO₄, 0.3 g Mg as MgSO₄, 4 H₂O as well as a micronutrient solution after Hoagland and 100 mg P as NaH₂PO₄ · 2 H₂O (P deficiency level). Four pots (four different cultivars) with 1000 mg P (optimum P supply) were used as control pots to characterize the relative yield potential of the treatment with P deficiency level (100 mg P). In each pot, five plants of one cultivar were grown to maturity with the soil being maintained at 70% of its maximum water holding capacity. Yield (grain and straw) and P content were determined and P removal and P harvest index calculated. There were four replicate pots of each cultivar.

2.3. Cultivation of plants until the stage of tillering

In this pot experiment, 24 cultivars were grown at two P levels with four replicates for 5 or 20 days (DC 25) in a growth chamber. As there was a shortage of seeds, Teo and Ultra were only grown at the low P level. Five plants (seed weight: 45–55 mg per seed) were grown in PVC vessels (diameter 9 cm, 40 cm height). The soil, nutrient and water supply were the same as above. The environmental conditions in the growth chamber were: photoperiods, 16 h; PAR, $300 \mu\text{E m}^{-2} \text{s}^{-1}$ (corresponding to about 25% of full daylight), 20°C, 80% relative humidity. At harvest, the dry weight of shoots and roots, P uptake, root length and acid phosphatase activity in the shoots were determined.

2.4. Measurements and plant analyses

2.4.1. Biomass

Shoots, roots, grains and straw were dried at 105°C for dry matter (dm) determination.

2.4.2. Content of phosphorus

Dried (105°C) and ground plant material was digested with HNO_3 in Teflon bombs at 180°C, and P was determined following Kitson and Mellon (1944). Phosphorus removal was calculated from the dry matter and P concentration.

2.4.3. Activity of acid phosphatases

The activity of the acid phosphatases (P_{ase}) characterising the P status of plants (Gransee, 1988) was determined following McLachlan (1980) and Gransee (1988). Samples of 1 g fresh matter of whole shoots were homogenized in 30 ml Tris-HCl buffer (pH 7.2). The filtrate was used as the enzyme assay. The hydrolysis of nitrophenyl-phosphate (NPP) to nitrophenol (measured at 405 nm) and phosphate at 37°C per unit time (total reaction time: 20 min) was taken as a measure of P_{ase} activity in $\text{nmol NPP g}^{-1} \text{shoot dry matter per second (nmol NPP g}^{-1} \text{s}^{-1})$. Shoot dm was determined in parallel samples.

2.4.4. Root length

The root length of all cultivars of the young low P plants was measured according to the method of Newman (1966) using a microscope and additionally with a special root counting device of the Comair Company (Melbourne). The root length of all cultivars of the young high P plants was measured for technical reasons by the Comair device only. Thus only nine cultivars of the low P and high P plants were counted with the same method. This fact was taken into account in the results shown in Table 3.

2.4.5. Phosphate influx

The P influx was expressed per unit root length (cm) and time (s) during a defined growth period. Young plants (four pots of each cultivar) were harvested at the 5th and 20th day of the growth period, and their P content (in roots and shoots) and root length were determined. With the knowledge of P uptake in 15 days and the assumption of an exponential root growth, the P influx can be calculated after Williams (1948):

$$\text{P influx} = \frac{U_2 - U_1}{t_2 - t_1} \times \frac{\ln(RL_2/RL_1)}{RL_2 - RL_1},$$

where U =P amount in shoots and roots at t_1 or t_2 , and RL =root length at t_1 or t_2 .

2.5. Statistical analysis

Differences among cultivars in the variables described above were evaluated by analysis of variance. If the F tests were significant, LSD ($P=0.05$) values were calculated. To test relationships among different variables, correlation coefficients were calculated.

3. Results

Plants in the pots with a high P supply (1000 mg P per pot) had twice the grain yield of those at a P supply of 100 mg P per pot (data not shown); i.e. the latter grew with an insufficient P supply.

Table 1 shows the results of measurements on these plants at maturity. Although only modern,

Table 1
Relative values of dry matter production, yield components, parameters of P metabolism and P efficiency of 24 spring barley cultivars at low P supply (mean = 100%)

Cultivar origin	Dry matter production				Yield components			P metabolism				P efficiency			
	Grain	Straw	Total dm	Harvest	Ears	Grains	Thousand	Grain	Grain	Straw	Straw	Total	P harvest	PEQ mg	P(dm)EQ mg
	plant ⁻¹ g	plant ⁻¹ g	plant ⁻¹ g	index	plant ⁻¹	plant ⁻¹	seed w. g	P conc. mg g ⁻¹	P content mg plant ⁻¹	P conc. mg g ⁻¹	P content mg plant ⁻¹	P uptake mg plant ⁻¹	index	grain mg P ⁻¹	dm mg P ⁻¹
Mean, absolute	4.38	4.13	8.51	0.52	5.01	23.5	37.4	1.75	7.66	0.27	1.12	8.77	0.87	500	875
Alexis, D	93	84	89	105	99	105	99	104	98	129	109	99	99	95	90
Apex, NL	99	107	103	96	105	99	94	100	99	100	108	100	99	99	103
Amazona, D	92	87	89	103	110	98	86	100	93	98	86	92	101	100	98
Aura, D	107	113	110	98	101	106	100	99	106	92	105	106	100	101	103
Baronesse, D	102	104	103	99	96	97	110	94	97	87	91	96	101	106	107
Berolina, A	108	102	105	103	103	96	110	101	109	101	103	109	101	99	97
Cerise, GB	97	88	93	104	101	95	100	96	92	93	84	91	102	106	101
Cheri, D	99	93	96	103	99	97	104	108	107	100	93	105	102	95	92
Cirstin, D	109	121	115	95	99	113	97	91	100	101	116	102	98	107	113
Comtesse, D	100	100	100	100	100	98	102	113	112	99	99	111	102	90	90
Defra, DDR	99	99	99	100	102	106	92	99	98	114	113	100	98	99	99
Europa, D	111	112	111	99	106	104	101	86	96	92	106	97	99	114	115
Gimpel, D	85	101	93	92	98	92	94	102	87	92	94	88	99	97	106
Golf, GB	109	104	107	102	110	97	102	93	101	112	116	103	98	105	103
Harry, S	102	101	101	101	83	112	110	101	103	101	102	103	100	99	98
Koral, CS	91	94	92	98	95	100	96	111	101	87	82	99	103	92	93
Perun, CS	93	86	89	104	91	101	100	106	99	91	78	96	103	97	93
Phantom, D	103	106	105	99	93	104	107	96	99	114	122	102	97	101	103
Princess, D	114	106	110	103	115	98	101	101	118	89	95	112	103	101	98
Rumba, D	99	101	100	99	97	105	95	99	98	102	103	99	99	101	102
Salome, DDR	96	95	96	100	106	92	99	104	99	94	90	98	101	98	97
Teco, GB	101	95	98	103	102	96	102	96	97	101	96	97	100	104	101
Toga, A	86	84	85	101	88	93	105	104	90	116	97	91	99	95	93
Ultra, D	105	118	111	94	104	105	95	99	103	96	113	105	99	100	106
LSD <i>P</i> = 0.05	17	16	16	5.5	19	16	11	14	18	30	34	18	4	14	14

high-yielding cultivars were used, there were differences in total dry matter yield: Toga gave 85%, and Cirstin gave 115% of the mean grain yield of all cultivars. The harvest index expressed as a percentage of the mean varied only between 92% (Gimpel) and 105% (Alexis). Some cultivars exceeded the mean grain yield by about 13% (Princesse, Europa). Others reached only 85% (Gimpel) of the mean grain yield. These differences were significant. The values of P uptake (grain and straw) and P utilization [PEQ, P(dm)EQ] were more variable (from 88 to a maximum of 115%) than the P harvest index, which varied only between 97 and 103% of the mean value of the cultivars. The differences in the case of P uptake were between 88% (Gimpel) and 112% (Princesse) and in the case of P utilization efficiency (PEQ) between 90% (Comtesse) and 114% (Europa). Grain yield was significantly correlated with total P uptake ($r=0.71^{***}$) and with P utilization efficiency (PEQ, $r=0.60^{**}$). The relation between grain yield and the PEQ or the P concentration in grains ($r=0.55^{**}$) was similar, which can be explained by the high P harvest index of spring barley: 87% of the P taken up was found in the grains. The correlation between grain yield and the P harvest index was small ($r=-0.14$). The relationships between grain yield and the P efficiency characters can be used to characterize cultivars: a low yield was associated with a low P uptake and medium utilization P efficiency (Gimpel, Amazone, Toga). A high yield was obtained either with high uptake and medium utilization P efficiency (Princesse, Berolina, Aura) or a medium uptake and high utilization P efficiency (Europa, Cirstin). The combination of high uptake and high utilization efficiency (implying a high grain yield) was not observed in the material investigated.

Fig. 1 shows how plant characters (based on the mean of all cultivars at DC 25) varied with P supply. It is striking that at the low P level, an almost similar total biomass was obtained, but a decrease of shoot biomass and an increase of root biomass and root length were observed. All features of P metabolism were decreased by a low P supply; only P_{ase} activity increased.

Table 2 shows that the reactions of the 22 culti-

vars to high and low P supply at the tillering stage were variable. Some cultivars had a high shoot dry matter at the high P level (Princesse, 112%; Berolina 111%) and also a relatively high dry matter at low P supply (114%, 116%, respectively). Other cultivars (e.g. Alexis) did relatively poorly with a low P supply (83% of mean), whereas Amazone did much better (from 90 to 112%). The same reaction was observed with the other characters. Regarding the P content of shoots, Berolina had a good rank position at both P levels, but Princesse lost its top position at the low P level (124 to 99%), whereas Amazone increased from 84 to 111%. Not all changes can be assessed here, but Table 3 demonstrates how each plant character changed in response to P fertilization. Only the root length and the P_{ase} activity showed significant r values, which means that the ranking of cultivars at the different P fertilization for both characters was relatively stable.

Table 4 shows the dependence of shoot dry matter and P removal on characters of P metabolism and root length, respectively, with a varying P supply. Shoot dry matter was significantly correlated with P uptake by the whole plant. With a low P supply, the root length seemed to be more important for shoot dry matter yield than with a high P supply. The same was found for the P content of the shoots.

Correlations were calculated between the characters of the plants grown with a low P supply until DC 25 and the grain yield and the P efficiency of mature plants (Table 5). All relationships were very weak. The closest relationships were found between grain yield, total dry matter or the P uptake at maturity and the dry matter yield of young shoots. However, only the latter relationship was statistically significant ($r=0.43$). The correlation between the PEQ and P_{ase} activity was almost significant at $P=0.05$.

4. Discussion

4.1. Variability of the P efficiency of spring barley

A high nutrient efficiency can be achieved by increasing nutrient uptake or the utilization effi-

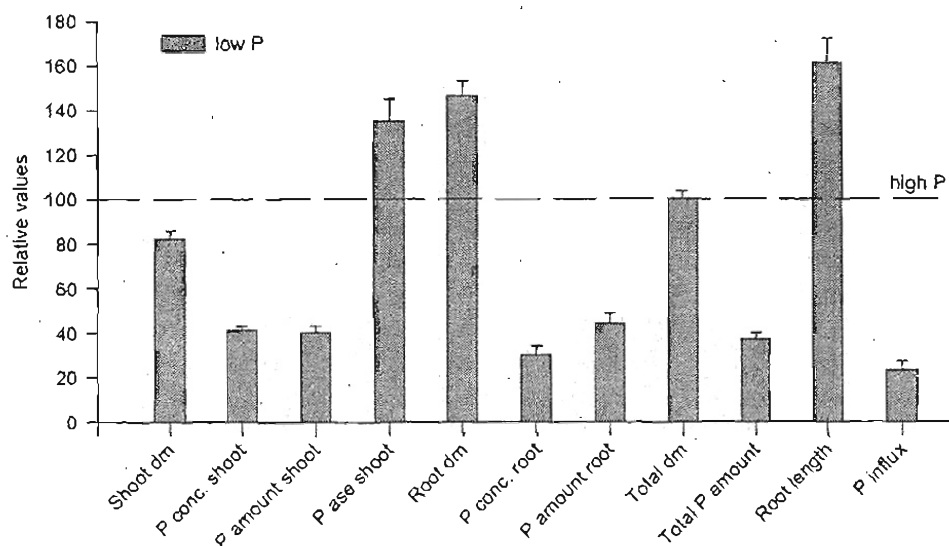


Fig. 1. Comparison of 11 characters from low P and high P-supplied plants at DC 25 (values of high P plants = 100%, bars = LSD at $P=0.05$).

ciency (Föhse et al., 1988). In the case of phosphorus, both ways are possible (Clark, 1983; Gabelman and Gerloff, 1983). Characters suitable for selection and genetic improvement have to show a sufficient genetical variability and heritability (Schinkel and Mechelke, 1990; Spanakakis, 1990). Under P deficiency (yield level: 50% of the maximum yield), significant differences in grain yield were observed. This result indicates that it should be possible to increase yield through a higher P efficiency by breeding, because both P uptake and PEQ varied significantly. A combination of a high P uptake with a high PEQ may be possible because no significant negative relationship existed between P uptake and PEQ ($r = -0.14$). Plants with a combination of the observed highest P uptake and the highest PEQ could theoretically reach a grain yield that is 27% higher than the average grain yield of all cultivars. This approach was also recommended by Sattelmacher et al. (1994). Other authors have reported a variability among cultivars in grain yield under P stress. This variability was also found for P uptake and PEQ (Nielsen and Schjorring, 1983; Batten, 1986; Jones et al., 1989; Helal, 1990). These reports and the results of this study suggest that there is a sufficient genetic variability in P uptake and utilization for further progress to be made by

breeding. This conclusion is based on the results of pot experiments in this study. As yet, no evidence of the genetic variation in field experiments has been obtained. However, in similar experiments with *Vicia faba* beans Stelling et al. (1996) found that the results obtained from the growth of inbred lines in pots and in the field were in good agreement.

4.2. Preselection for P efficiency at the seedling stage

For practical breeding, the question arises as to whether a selection of P efficiency at the seedling stage is possible and which characters could be used as selection criteria. Table 5 shows that only very weak relationships existed between biomass, root length and the P metabolism of the young plants and grain yield, total dm, P uptake and P utilization (PEQ) of plants grown to maturity. The relationship between the shoot biomass of young plants and the grain yield was positive but nevertheless very weak with $r = 0.37$.

One reason for the weak relations in Table 5 could be the different temporal adaptation of the cultivars to P starvation conditions. It was shown that no difference existed between the root length at high or low P supply after 5 days' growth (not

Table 2
Six plant parameters of young plants (DC 25) of 24 barley cultivars at high P (+P) and low P (–P) supply

Cultivar	Shoot dm mg plant ⁻¹		Shoot P conc. mg g ⁻¹		Shoot P amount mg plant ⁻¹		Shoot P _{acc} act. μmol g dm ⁻¹ s ⁻¹		Root length cm plant ⁻¹		P influx, day 5–20 10 ⁻¹⁴ mol P cm ⁻¹ s ⁻¹	
	+P	–P	+P	–P	+P	–P	+P	–P	+P	–P	+P	–P
Mean	300	248	6.1	2.5	1.84	0.63	1098	1467	2496	3995	9.0	2.1
Mean rel.	100	100	100	100	100	100	100	100	100	100	100	100
Alexis	98	81	91	97	89	78	78	106	88	83	94	84
Apex	106	100	107	106	114	106	102	102	133	96	87	110
Amazonc	90	112	93	99	84	111	95	96	110	122	88	95
Aura	96	93	97	109	94	102	97	95	95	92	102	104
Baronesse	86	89	122	115	105	103	84	87	87	84	105	129
Berolina	111	116	99	100	109	117	82	75	101	113	107	101
Cerise	92	79	101	106	92	83	152	143	87	72	96	118
Cheri	98	98	107	108	105	105	78	83	91	106	109	99
Cirstin	109	110	88	82	96	91	96	92	111	99	90	88
Comtesse	89	102	104	104	92	106	110	86	105	104	86	104
Defra	103	90	87	100	90	91	87	68	95	103	96	89
Europa	97	100	101	95	98	96	101	124	94	101	108	85
Gimpel	104	89	102	114	106	101	75	71	107	104	97	99
Golf	101	105	94	92	95	97	183	191	95	89	99	106
Harry	99	94	90	93	89	88	114	129	123	94	81	94
Koral	95	110	103	87	97	98	79	89	94	97	102	98
Perun	103	108	98	107	100	116	97	91	90	100	96	119
Phantom	105	109	93	100	91	109	88	79	83	107	108	105
Princesse	112	114	111	87	124	99	114	115	115	111	113	95
Rumba	113	98	98	100	111	99	104	97	103	105	111	98
Salome	106	108	113	99	120	109	84	94	88	109	122	99
Teo	—	104	—	105	—	110	—	78	—	101	—	106
Toga	99	91	99	93	97	86	94	109	105	109	100	76
Ultra	91	—	103	—	102	—	109	—	96	—	107	—
LSD <i>P</i> = 0.05	26	35	18	19	28	38	31	23	48	39	33	38

Table 3
Correlation coefficients between the given plant characters at low and high P at DC 25 (*n* = 22 cv. without Teo, Ultra)

Total dm	0.32
Shoot dm	0.41
Root dm	0.08
P conc. shoot	0.41
P content shoot	0.35
P conc. root	0.36
P content root	–0.17
P uptake	0.26
Root length ^a	0.71*
P influx ^a	0.04
P _{acc} activity shoot	0.89***

^a*n* = 9.

*Significant at *P* = 0.05.

***Significant at *P* = 0.001.

shown in Fig. 1). Therefore, the differences must have developed later. It is also possible that the adaptation was not achieved after 20 days. The comparison between shoot dry matter from young plants with the grain yield of these cultivars shows that some cultivars have developed high shoot dry matter as young plants, e.g. cultivars Princesse, Berolina or Cirstin. Others, however, e.g. cultivars Aura, Golf and Europa with only medium shoot biomass developed high grain yields. The conclusion is that cultivars exist that can adapt relatively well to P starvation conditions after DC 25. Weak relationships between the biomass of young plants and grain yields or dry matter yields at maturity were also observed by Leon et al. (1989) for maize and by Thung (1990) for *Phaseolus* beans. The uptake of P can also vary among cultivars during

Table 4
Correlation coefficients (r) between shoot dry matter (dm) or shoot P amount and some plant characters at high and low P supply at DC 25 ($n=23$)

Dependent variable	Explanatory variable	High P	Low P
		r	r
Shoot dm	P amount in shoot + root	0.62**	0.58**
	Root length	0.30	0.67***
	P influx	0.28	0.01
	P conc. shoot	-0.23	-0.41*
	P conc. root	-0.04	0.04
	P_{ase} activ.	-0.08	-0.37
P content of shoots	P_{ase} activ.	-0.14	-0.43*
	Root length	0.10	0.43*
	P influx	0.62**	0.46*

*Significant at $P=0.05$.

**Significant at $P=0.01$.

***Significant at $P=0.001$.

the growth period (Nielsen and Schjorring, 1983). Horst and Wiesler (1986) showed for two spring wheat cultivars grown under limited P conditions that one cultivar that had a low dry matter and P uptake at shooting had to compensate for flowering.

The significant differences in P uptake and P utilization by young plants of different cultivars did not automatically show a close relationship to grain yield and P efficiency at maturity, because growth and nutrient uptake until maturity of the different cultivars changed considerably. The results of a test at DC 25 for an assessment of P efficiency are applicable only to this stage and do not necessarily indicate P efficiency of the later growth stages.

4.3. Selection characters

Gransee (1988) found a close negative correlation between the P_{ase} activity of young barley shoots and the produced grain yields produced under a varying P supply. According to these results, the conclusion could be drawn that cultivars with a low phosphatase activity at an early stage reflect a sufficient P supply and high grain yields and vice versa. Thus, the activity of the acid phosphatases could be a useful selection criterion for the utilization P efficiency, as proposed by Thung (1990) and Vose (1990). Our results, however, showed only a weak though positive relationship between the activity of the acid phosphatases of P starved young plants and the grain yield of

Table 5
Correlation coefficients between characters measured on young low P plants (DC 25) and mature low P plants (DC 92), $n=23$

Characters of young plants (DC 25)	Characters of mature plants (DC 92)			
	Grain yield	Total dm	P uptake	PEQ
Shoot dm	0.37	0.34	0.43*	0.01
P conc. shoot	-0.30	-0.25	-0.27	-0.10
P uptake	0.04	0.04	0.15	-0.11
Root length	-0.04	-0.03	0.14	-0.23
P influx	0.08	0.05	-0.02	0.15
P_{ase} activ.	0.28	0.15	0.02	0.37

*Significant at $P=0.05$.

plants that grew under the same P conditions. Therefore, P_{asc} cannot be used reliably for the selection of P efficiency.

Beside P_{asc} activity, the root length was one of the characters exhibiting a large genetic variation. Between root length and the P uptake of the shoot of young plants under P stress, a significant relationship was detected. Between root length and grain yield, however, no significant relationship was found. Is root length nevertheless a criterion of selection for P efficiency? With a high P supply, each root system is able to take up enough P for sufficient plant growth. With a low P supply, the influx per unit root and time is very low. A large root surface area and a large root–shoot ratio favour P uptake, and there is a more satisfactory P supply of the plant (Föhse et al., 1988). Young cereal plants in particular need a sufficient amount of phosphorus for the development of tillers and spikelets (Römer and Schilling, 1986; Römer and Schilling, 1992). High yielding varieties may have a better chance on soils of low P availability if they are able to develop an expanded root system. As 30% of the genome is associated with the development of the root system (Zobel, 1975), it may be possible to select varieties with a high root surface area.

Acknowledgment

This contribution is dedicated to Prof. Dr. Günther Schilling, Halle, on the occasion of his 65th birthday.

References

- Bänzinger, M., Feil, B., Schmidt, J.E., Stamp, P., 1992. Genotypic variation in grain nitrogen content of wheat as affected by mineral nitrogen supply in the soil. *Eur. J. Agron.* 1 (3), 155–162.
- Batten, G.D., 1986. The uptake and utilization of phosphorus and nitrogen by diploid, tetraploid and hexaploid wheats (*Triticum* spp.). *Ann. Bot.* 58, 49–59.
- Baumer, M., Göppel, W., 1990. Verzeichnis der Winter- und Sommergerstensorten, (Ed.), Bayerische Landesanstalt für Bodenkultur und Pflanzenbau, Freising, Germany.
- Clark, R.B., 1983. Plant genotype differences in the uptake, translocation, accumulation, and use of mineral elements required for plant growth. *Plant Soil* 72, 175–196.
- El Bassam, N., 1989. Genotype response of barley to nitrogen—A contribution towards characterization and identification of low-input-genotypes. In: XII. Eucarpia Congress, pp. 23–26.
- Feil, B., 1990a. Der Zuchtfortschritt bei Getreide. Teil 1: Ertrag und Ertragsstruktur alter und neuer Getreidesorten. *Kalibriefe* 20 (3), 213–223.
- Feil, B., 1990b. Der Zuchtfortschritt bei Getreide. Teil 2: Physiologische und morphologische Merkmale alter und neuer Sorten. *Kalibriefe* 20 (3), 225–240.
- Feil, B., 1992. Breeding progress in small grain cereals—a comparison of old and modern cultivars. *Plant Breed.* 108, 1–11.
- Föhse, D., Claassen, N., Jungk, A., 1988. Phosphorus efficiency of plants. *Plant Soil* 110, 101–109.
- Gabelman, W.H., Gerloff, G.C., 1983. The search for and interpretation of genetic controls that enhance plant growth under deficiency levels of a macronutrient. *Plant Soil* 72, 335–350.
- Gransee, A., 1988. Überwachung des P-Ernährungszustandes wachsender Getreidebestände unter Nutzung von P-Fraktionen und Enzymaktivitäten der Pflanze. Dissertation, Universität Halle-Wittenberg.
- Helal, H.M., 1990. Zur Phosphorausnutzungs-Effizienz verschiedener Sorten von Sommerweizen. *VDLUFA-Schriftenreihe* 32, 315–319.
- Horst, W.J., Wiesler, F., 1986. Genotypische Unterschiede in den Ansprüchen an das Phosphat-Angebot bei Sommerweizen. *VDLUFA-Schriftenreihe* 20, 175–190.
- Jones, G.P.D., Blair, G.J., Jessop, R.S., 1989. Phosphorus efficiency in wheat—A useful selection criterion? *Field Crops Res.* 21, 257–264.
- Kitson, R.E., Mellon, M.G., 1944. Colorimetric determination of phosphorus as molybdovanado phosphoric acid. *Industr. Engng Chem. Anal.* 16, 379–383.
- Leon, J., Geisler, G., Thiraporn, R., Stamp, P., 1989. Genotypic variation in maize shoot biomass at different stages of development. *Plant Breed.* 103, 181–189.
- McLachlan, K.D., 1980. Acid phosphatase activity of intact roots and phosphorus nutrition of plants. I. Assay conditions and phosphatase activity. *Aust. J. Agric. Res.* 31, 429–440.
- Newman, E.J., 1966. A method of estimating the total length of root in a sample. *J. Appl. Ecol.* 3, 133–145.
- Nielsen, N.E., Schjorring, J.K., 1983. Efficiency and kinetics of phosphorus uptake from soil by various barley genotypes. *Plant Soil* 72, 225–230.
- Pagel, H., Enzmann, J., Mütscher, H., 1982. Pflanzennährstoffe in tropischen Böden—ihre Bestimmung und Bewertung. VEB Deutscher Landwirtschaftsverlag, Berlin.
- Römer, W., Schilling, G., 1986. Phosphorus requirement of the wheat plant in various stages of its life cycle. *Plant Soil* 91, 221–229.
- Römer, W., Schilling, G., 1992. Experimentelle Befunde und Überlegungen zur Phosphatdüngung in der Zukunft—Übersichtsbeitrag. *Arch. Acker- Pflanzenbau Bodenkd.* 36, 235–248.
- Römer, W., Beißner, L., Schenk, H., Jungk, A., 1995. Einfluß von Sorte und Phosphordüngung auf den Phosphorgehalt

- und die Aktivität der sauren Phosphatasen von Weizen und Gerste. *Z. Pflanzenernähr. Bodenk.* 158, 3–8.
- Sanchez, P., 1976. *Properties and Management of Soils in the Tropics*. Wiley, New York.
- Sattelmacher, B., Horst, W.J., Becker, H.C., 1994. Factors that contribute to genetic variation for nutrient efficiency of crop plants. *Z. Pflanzenernähr. Bodenk.* 157, 215–224.
- Schinkel, B., Mechelke, W., 1990. A method to estimate the prospect of specific breeding for nutrient efficiency. In: El Bassam, N., Dambroth, M., Loughman, B.C. (Eds.), *Genetic Aspects of Plant Mineral Nutrition*. Dordrecht/Boston, Kluwer Academic Publishers, pp. 449–456.
- Schüller, H., 1969. Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphats in Böden. *Z. Pflanzenernähr. Bodenk.* 123, 48–63.
- Spanakakis, A., 1990. Grain yield and quality characters of genotypes in F_3 generation under low and high nitrogen input. In: El Bassam, N., Dambroth, M., Loughman, B.C. (Eds.), *Genetic Aspects of Plant Mineral Nutrition*. Dordrecht/Boston, Kluwer Academic Publishers, pp. 457–464.
- Stelling, D., Wang, S.H., Römer, W., 1996. Efficiency in the use of phosphorus, nitrogen and potassium in topless faba bean (*Vicia faba* L.)—variability and inheritance. *Plant Breed.* 115, 361–366.
- Thung, M., 1990. A limiting nutrient in bean (*Phaseolus vulgaris* L.) production in Latin America and field screening for efficiency and response. In: El Bassam, N., Dambroth, M., Loughman, B.C. (Eds.), *Genetic Aspects of Plant Mineral Nutrition*. Dordrecht/Boston, Kluwer Academic Publishers, pp. 501–521.
- Vose, P.B., 1990. Screening techniques for plant nutrient efficiency: Philosophy and methods. In: El Bassam, N., Dambroth, M., Loughman, B.C. (Eds.), *Genetic Aspects of Plant Mineral Nutrition*. Dordrecht/Boston, Kluwer Academic Publishers, pp. 283–289.
- Williams, R.F., 1948. The effects of phosphorus supply on the rates of intake of phosphorus and upon certain aspects of phosphorus metabolism in gramineous plants. *Aust. J. Sci. Res.* 1, 333–361.
- Yau, S.K., Thurling, N., 1987. Genetic variation in nitrogen uptake and utilization in spring rape (*Brassica napus* L.) and its exploitation through selection. *Plant Breed.* 98, 330–338.
- Zatoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. *Weed Res.* 14, 415–421.
- Zobel, R.W., 1975. The genetics of root development. In: Torrey, J.G., Clarkson, D.T. (Eds.), *The Development and Function of Roots*. Academic Press, London, pp. 261–275.