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Variation in acquisition of soil phosphorus among wheat and barley genotypes

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Abstract

To assess the extent of variation in phosphorus acquisition efficiency of some winter wheat (*Triticum aestivum* L.), winter and spring barley (*Hordeum vulgare* L.) genotypes, depletion of inorganic phosphorus (P) extractable with 0.5 *M* $NaHCO_3$ ($NaHCO_3$-P_i) from the rhizosphere soil was studied. Nutrients supply, rhizosphere soil pH and soil water content was kept equal for all the genotypes with the aim to reduce the confounding variation due to these factors. The experimental set up implied that no difference in the relative growth rates, nitrogen, potassium and calcium content of shoot dry matter occurred among the genotypes.

The winter wheat, winter barley and spring barley genotypes differed significantly ($p>0.05$) in their efficiency to acquire $NaHCO_3$-P_i from the rhizosphere soil. The efficiency of the winter wheat genotypes to acquire $NaHCO_3$-P_i from rhizosphere soil ranked Kraka > Gawain > Foreman > Sleipner = Obelisk > Kosack > Pepital > Arum. Winter wheat genotypes differed in extent of P depletion profiles in the rhizosphere, indicating variation in root hair length. The winter barley and spring barley genotypes also showed significant differences in their P depletion profiles near roots. The efficiency of the winter barley genotypes to acquire soil P in the rhizosphere ranked Hamu > Frost > Marinka > Astrid > Clarine = Angora. The efficiency of spring barley genotypes to acquire $NaHCO_3$-P_i in the rhizosphere ranked Canut > Etna ≅ Riga > Digger > Peel > Semal > Alexis. The rhizosphere pH remained unchanged, suggesting that additional mechanisms such as root hair formation and root exudates play a significant role in causing variation in P acquisition among the genotypes.

Introduction

The possibility of exploiting genotype differences for improving nutrient efficiency of crop plants has received increased attention in recent years (Baligar and Duncan, 1990; Gerlof and Gabelmann, 1983; Schjørring and Nielsen, 1987). Phosphorus (P) efficient genotypes can be useful for maintaining high productivity in low input agriculture. From mineral nutrition point of view, a genotype is more efficient than others if it mobilizes and absorbs more P from soils (P acquisition efficiency) and/or makes better use of the absorbed P to produce biomass (P use efficiency). Improvement of phosphorus efficiency of crop plants by selection seems possible (Caradus, 1994). Additional breeding of new crop genotypes with improved P efficiency may be a supplementary alternative for reducing the traditional amendments of soils by the applications of fertilizers (Batten, 1992). For successful exploitation of such alternative approaches, the knowledge on the extent of genetic variation among the existing genotypes appears to be a primary step (Mahon, 1983).

The extent of variability among crop plants to acquire soil P is influenced by both genetic and environmental factors (Nielsen, 1983). This makes it difficult to assess genetical superiority of germplasms (Mahon, 1983). Selection under controlled conditions in solution cultures has been suggested (Wild et al., 1987) to reduce environmental effects. This approach is useful for studying P-use efficiency result-

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ing from superior translocation (Marschner, 1995) and favourable partitioning between organic and inorganic P forms in plants (Elliott and Lauchli, 1985). However, for nutrients of low mobility in soil such as phosphorus, additional root induced mechanisms determining efficiency of P acquisition may be operating largely at soil-root interface (Graham, 1984).

Phosphorus acquisition efficiency is influenced by size and distribution of root system (Nielsen, 1979; Noordwijk et al., 1990; O'Toole and Bland, 1987), root hairs (Föhse et al., 1991; Lewis and Quirk, 1967), kinetic uptake parameters (Nielsen and Barber, 1978), root-induced pH change (Gahoonia and Nielsen, 1992a; Gahoonia et al., 1992), root exudation (Bar-Yosef, 1991; Marschner, 1995), and soil moisture (Gahoonia et al., 1994). Phosphorus supply in turn influences root growth and root hair formation (Föhse and Jungk, 1983), rate of root exudation (Hoffland et al., 1989), ratio of nitrate and ammonium uptake by reducing only nitrate absorption (Schjørring 1986), root induced pH changes (Grinstad et al., 1982; Moorby et al., 1985) and phosphatase activity near roots (Silberbush et al., 1981). Hence, in attempt to assess variability in acquisition of soil P among crop genotypes, it is desirable to reduce confounding effects of environmental and nutritional factors.

Slow diffusion of P results in depletion of P in soil near absorbing roots. The P depletion profiles in soil close to root mats of equal surface area can be studied by thin slicing technique (Gahoonia and Nielsen, 1991). In addition, soil moisture and nutrients supply can be controlled and rhizosphere pH can be kept fairly unchanged (Gahoonia and Nielsen, 1992). Variation in P depletion profiles may then provide information on the acquisition efficiency of the genotypes. This paper reports results on the extent of variation in phosphorus acquisition from the rhizosphere soil of some wheat and barley genotypes.

Materials and methods

Soil

A Danish top soil was used having the following properties:

Coarse sand 28%, fine sand 34%, silt 18%, clay 20%, organic matter 1.9%, pH 6.3 in 5 m*M* NO_3 (because it did not differ significantly from pH in $CaCl_2$, and had smaller measurement error allowing to measure small pH differences), CEC 17 meq $100g^{-1}$ soil at pH 7, total P = 22.2 μmoles P cm^{-3}, inorganic P extractable with 0.5 *M* $NaHCO_3$ = 1.40 moles P cm^{-3}, concentration of P in soil solution = 7 μM.

Table 1. Overview of parental germplasm of cereal genotypes studied

Winter wheat (*Triticum aestivum* L.)	
Arum	Galahad × 487
Foreman	Mitras × Hobbit-Hodgehog line
Gawain	Dunn derivative × Brigand
Kosack	(Mironovskaja 808 × Starke M) × Holme M
Kraka	Kranich × Caribo
Obelisk	chosen by composite cross
Pepital	ROC 109-75 × VDHO4O-71 B
Sleipner	W.20102-CB.149-Huntsman × Biblo
Winter barley (*Hordeum vulgare* L.)	
Angora	Breun Stamm 301a × Wheinst. W 5907
Astrid	Weib.8264 × Weib.5907
Clarine	Igri × Mogador
Frost	Pella × Astrix
Hamu	Mammut × Hasso
Marinka	(Alpha × Sv.P67.4) × Malta
Spring barley	
Alexis	Breun St.1622d × Triumph
Canut	Triumph × Magnum
Digger	(Magnif E 105 × Univers) × Aramir
Etna	Magnum × Alis Abed (NRPB)[a]
Peel	Regatta × (VSB 10-15-80 × NFC 1440–80)
Riga	Magnum × Alis Abed (Abed)[b]
Semal	Sj. 746570 × Triumph

[a]NRPB : Nicikerson RPB Limited, Rothwell, GB-Lincoln LN7 6DT.
[b]Abed: Abed Planteavlsstation, Abedvej 39, DK 4920 Søllested.

Genotypes

Cereal genotypes (Table 1) were chosen in cooperation with Danish Agricultural Advisory Centre, based on cultivated area, variation in parental germplasm and yield. Spring barley genotypes Etna and Riga originated from same parental germplasm, providing an additional check on the ability of germplasms to acquire soil P. The genotypes were pregrown in vermiculite filled in PVC tubes (length 10 cm, diameter 4.4 cm) closed at the bottom by nylon cloth impervious to roots. Two ceramic fibre wicks were placed along the inner sides of the tubes to supply

nutrient solution of defined composition. The genotypes having uniformly developed root mats (12 days after germination) were transplanted into soil columns filled into PVC tubes (length 3 cm, diameter 5.6 cm). The soil columns were separated by a nylon screen of mesh size 43 μm into 3 cm test soil columns below and 1 cm soil layer above the screen (Gahoonia and Nielsen, 1991). The soil columns (bulk density 1.3 g cm^{-3}) were maintained at defined moisture (Θ = 0.21) by placing them over small cup-shaped sand baths each fitted with a wick dipping into reservoir of distilled water. After transplantation, new root mats developed over the nylon mesh, representing a root surface area of 24.6 cm^{-2}. Due to geotropic nature of root growth mostly the "active" apical root zones covered the nylon mesh (open space 22%), but root hairs penetrated into the soil. The supply of external nutrient solution (16.2 m*M* total-N of which 13 m*M* NO_3-N and 3.2 m*M* NH_4-N; 0.54 m*M* P, 0.61 m*M* S, 7.16 m*M* K, 1.4 m*M* Ca, 0.35 m*M* Mg, 0.24 m*M* Na, 0.4 m*M* Cl, 15.2 μ*M* Fe,12.2 μ*M* n, 0.88 μ*M* Cu, 4.6 μ*M* B and 0.14 μ*M* Mo) to the plant roots in vermiculite was continued via the two wicks at 20 cm water tension. The ratio of nutrients in the supplied solution was adjusted to match the nutrient ratio in dry matter of monocot plant species. Based on previous studies (Gahoonia and Nielsen, 1991, 1992) the concentration was expected to create moderate P deficiency and to avoid deficiencies of other nutrients at relative growth rate (RGR) of 0.15 day^{-1}. The water uptake from the external nutrient solution was expected to be almost equal, maintaining equal supply of nutrients to all the genotypes. Water uptake also occurred via the soil columns (10 $\pm$2% of the total water uptake). The percentage of total N as ammonium in the supply solution was adjusted to maintain rhizosphere soil pH fairly unchanged (Gahoonia and Nielsen, 1992). The experiments were conducted under controlled conditions (light intensity 400 μE s^{-1} m^{-2}, light/dark period 16/8 h, temperature 19/15 °C, relative humidity 75%). More details of the plant growing technique and rhizosphere pH control are given in Gahoonia and Nielsen (1991, 1992). After 14 days soil columns were separated from root mats, quickly frozen in liquid nitrogen and sliced with freezing microtome to obtain rhizosphere soil samples of distances 0.019, 0.038, 0.094, 0.144, 0.194, 0.244 and 0.294 cm.

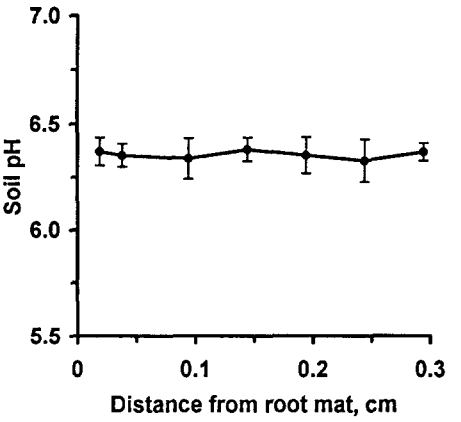

Fig. 1. The soil pH in the rhizosphere of wheat and barley genotypes.

Analytical procedures

Phosphorus analysis of rhizosphere soil

To 0.5 g of soil in a centrifuge tube, 5 mL, of 0.5 *M* $NaHCO_3$ (pH 8.5), was added. The tubes were shaken for 2.0 hours. Inorganic P ($NaHCO_3$-P_i) in the supernatant was determined immediately by the method of Murphy and Riley (1962). Unplanted standard soil was also analyzed each time P analysis of the rhizosphere soil samples was performed.

The quantity of $NaHCO_3$-P_i depleted $Q(NaHCO_3\text{-}P_i)_d$ was calculated by integrating the area under the respective depletion profile. Total quantity of inorganic P extractable with 0.5 *M* $NaHCO_3$, $Q(NaHCO_3\text{-}P_i)_t$ in the rhizosphere soil was 10 μmoles, calculated from initial $NaHCO_3$-P_i concentration in bulk soil (1.40 μmoles P cm^{-3}), contact surface area between the soil columns and the root mats (24.6 cm^2) and the extent of rhizosphere soil (0.294 cm), beyond which $NaHCO_3$-P_i was not depleted by most of genotypes.

The efficiency (E) to acquire $NaHCO_3$-P_i from the rhizosphere soil was calculated as

$$E = 100\frac{Q(NaHCO_3 - P_i)_d}{Q(NahCO_3 - P_i)_t} \qquad (1)$$

From the quantity of P depleted, mean net influx ($\bar{F}_n$) per cm^{-2} root mat in time t can be calculated as follow,

$$\bar{F}_n \cong Q(NaHCO_3 - P_i)_d/24.6t \qquad (2)$$

Plant material (shoot) was dried at 80 °C to constant weight and analyzed for N, P, K and Ca.

Table 2. Shoot dry matter (DM) relative growth rate (RGR) and phosphorus (P) and nitrogen (N) content of plant dry matter of cereal genotypes in 14 days

Genotypes	DM (g)	RGR (d^{-1})	%P	%N
Winter wheat				
Arum	3.5±0.2	0.14±0.01	0.63±0.04	4.3±0.1
Foreman	3.3±0.1	0.13±0.02	0.52±0.05	4.3±0.2
Gawain	3.2±0.3	0.14±0.01	0.64±0.04	4.2±0.1
Kosack	3.6±0.3	O.13±0.01	0.61±0.05	4.2±0.2
Kraka	3.4±0.2	0.16±0.02	0.53±0.04	4.2±0.1
Obelisk	3.2±0.1	0.15±0.01	0.62±0.03	4.2±0.1
Pepital	3.4±0.1	0.15±0.02	0.53±0.06	4.4±0.1
Sleipner	3.6±0.2	0.14±0.01	0.62±0.04	4.3±0.2
Winter barley				
Angora	3.4±0.1	0.15±0.02	0.53±0.08	4.3±0.1
Astrid	3.2±0.2	0.13±0.01	0.55±0.07	4.0±0.1
Clarine	3.1±0.1	0.13±0.01	0.62±0.06	4.2±0.3
Frost	3.1±0.3	0.14±0.02	0.63±0.06	4.2±0.2
Hamu	3.2±0.2	0.14±0.01	0.63±0.03	4.3±0.3
Marinka	3.5±0.1	0.15±0.02	0.57±0.04	4.1±0.1
Spring barley				
Alexis	3.2±0.2	0.15±0.02	0.56±0.16	3.8±0.2
Canut	3.4±0.3	0.15±0.01	0.62±0.10	3.6±0.2
Digger	3.1±0.2	0.14±0.01	0.65±0.15	3.5±0.1
Etna	3.3±0.1	0.16±0.01	0.67±0.12	3.8±0.3
Peel	3.2±0.3	0.14±0.02	0.51±0.11	3.6±0.1
Riga	3.4±0.2	0.15±0.02	0.65±0.12	3.6±0.1
Semal	3.3±0.1	0.16±0.01	0.54±0.13	3.5±0.2

Table 3. The supply of nitrogen (N), Potassium (K), Calcium (Ca) and phosphorus (P) from the external nutrient solution and uptake of nutrients

	N	K	Ca	P
	mmol d^{-1}			
Supply	1.05	0.46	0.09	0.035
Uptake	1.20	0.49	0.15	0.10

Results

The water uptake from the external nutrient solution (65 ± 6 mL day^{-1}) and via the soil columns (5.8 ± 1.8 mL day^{-1}) did not differ significantly (p>0.05) among

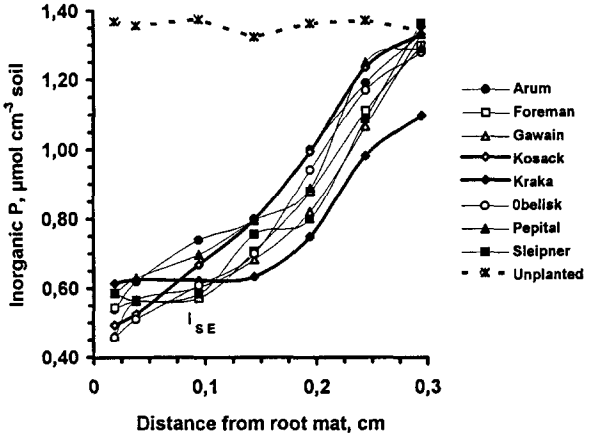

Fig. 2. Depletion profiles of inorganic phosphorus extractable with 0. 5 *M* $NaHCO_3$ in the rhizosphere of winter wheat genotypes in 14 days with fairly unchanged rhizosphere pH.

the genotypes, maintaining equal nitrogen (Table 2), potassium (K = 3.9 ± 0.3%) and calcium (Ca =1.2 ±0.2%) concentration in shoot dry matter. The equal water uptake via the soil columns also indicated equal contact between the soil columns and root mats of genotypes. The relative growth rates of winter wheat, winter barley and spring barley did not differ significantly (Table 2). The supply of other nutrients (for example N, K, Ca in Table 3) except P was met from the external nutrient solution. The rhizosphere pH remained fairly unchanged (Fig. 1). In all cases equal root surface area (root mat of 24.6 cm^2) was in contact with soil columns of defined moisture content. Thus, the experimental set up provided comparable conditions to assess genotypic variability in P depletion profiles in the rhizosphere and to reduce the effect of rhizosphere pH.

Phosphorus depletion profiles differed significantly (p>0.05) in the rhizosphere of winter wheat genotypes (Fig. 2). The pattern of depletion profiles differed in depth and extent of depletion zones. For example, the concentration of P near the root mat of Kosack decreased up to 0.48 μmoles cm^{-3} and that of Kraka up to 0.60 μmoles cm^{-3}. At 0.15 cm from the root mat P concentrations in case of Kosack increased up to 0.80 μmoles cm^{-3} whereas with Kraka it remained unchanged. Thus, Kosack was able to reduce soil P concentration near the roots to lower level whereas Kraka extended the effective volume of soil close to the roots. Kraka depleted nearly 20% more P than Kosack.

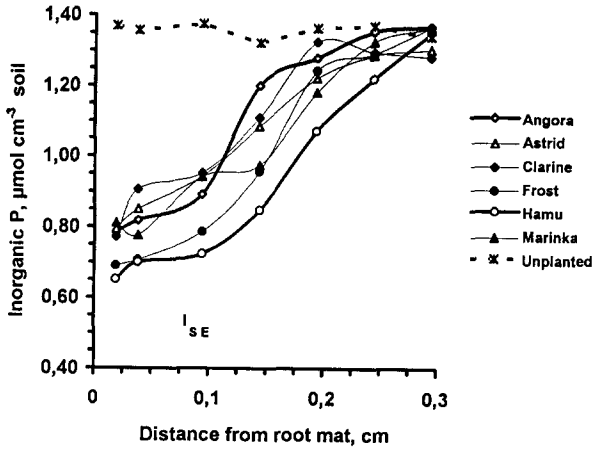

Fig. 3. Depletion profiles of inorganic phosphorus extractable with 0.5 *M* $NaHCO_3$ in the rhizosphere of winter barley genotypes in 14 days with fairly unchanged rhizosphere pH.

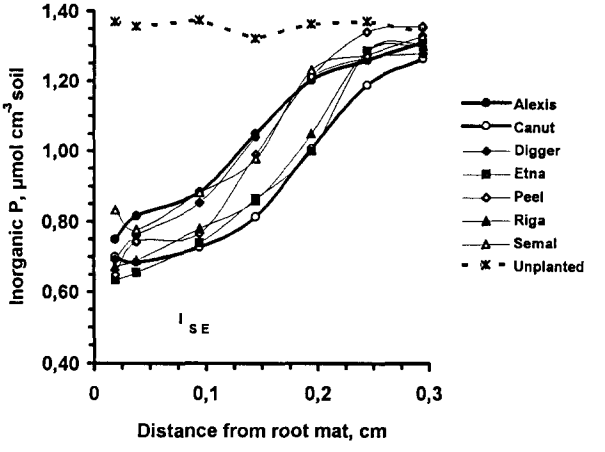

Fig. 4. Depletion profiles of inorganic phosphorus extractable with 0. 5 *M* $NaHCO_3$ in the rhizosphere of spring barley genotypes in 14 days with fairly unchanged rhizosphere pH.

The P depletion profiles in the rhizosphere of winter barley (Fig. 3) and spring barley genotypes (Fig. 4) also differed significantly (p>0.05), but the pattern of the profiles was mostly parallel. Among the winter barley genotypes, Hamu was the most efficient, depleting nearly 60% more P than Angora (Fig. 3). The most efficient spring barley genotype Canut also depleted nearly 60% more P than the least efficient Alexis (Fig. 4).

The P concentration in shoot dry matter (Table 2) and the quantity of P depleted from the rhizosphere soil and mean net influx ($\bar{F}_n$) of P (Table 4) differed significantly (p>0.05) among the investigated genotypes.

The efficiency to acquire $NaHCO_3$-P_i from the rhizosphere soil varied widely among the investigated cereal genotypes (Table 4) as calculated from equation 1. The efficiency to acquire $NaHCO_3$-P_i from the rhizosphere soil ranked Kraka > Gawain > Foreman. > Sleipner = Obelisk > Kosack > Pepital >Arum for winter wheat genotypes. For barley genotypes the efficiency to acquire soil P in the rhizosphere ranked Hamu > Frost > Marinka > Astrid > Clarine = Angora for winter barley; and Canut > Etna > Riga > Diggel- > Peel > Semal > Alexis for spring barley (Table 4).

Discussion

Phosphorus acquisition efficiency of cereal genotypes was investigated by applying a technique in which root surface is represented by a root mat (mainly the "active" apical root zones) in contact with soil in plane geometry. Plant roots under natural growing conditions will have cylindrical root-soil contact. Root size and its distribution is important for P acquisition (Noordwijk et al., 1990) and crop genotypes may differ in root size (Schjørring and Nielsen, 1987). The experimental approach applied here made use of the basic definition of rhizosphere soil, e.g. the zone of soil influenced by roots; providing the possibility to investigate acquisition of soil P very close to the roots of genotypes growing under defined nutritional and rhizosphere conditions; and by maintaining equal root surface. The genotypes were kept at desired nutritional status by external nutrient supply. The P in shoot dry matter (DM) of the genotypes (Table 2) was close to the P content of moderate P deficient young cereal plants when considered as function of N concentration in DM (Møller-Nielsen and Friis Nielsen, 1976).

The investigated cereal genotypes varied in depletion of soil phosphorus in their rhizosphere (Figs. 2, 3, 4). The variation was observed both in reduction of P concentration at the root mat surface and in extension of depletion profiles. Rhizosphere pH change caused by nitrogen source influences the acquisition of soil phosphorus in the rhizosphere (Gahoonia and Nielsen, 1992a) and variation in the ability of wheat and barley genotypes to change rhizosphere pH has been observed (Gollany and Schumacher, 1993). In the present investigation the rhizosphere pH remained unchanged (Fig. 1), suggesting that additional mechanism such as root exudation, enhancing solubility of soil P close to roots (Earl et al., 1979; Jones and Darrah, 1994; Nagarajah et al., 1968) play a significant role in P acquisition efficiency of the genotypes. Variation in root exudation depends on P nutrition status of plants (Hoffland

Table 4. The quantities of $NaHCO_3$-P_i)) depleted near root mats $Q(NaHCO_3\text{-}P_i)_d$ in 14 days, mean net influx ($\bar{F}_n$) and efficiency (E) of cereal genotypes to deplete P from rhizosphere soil. Total inorganic P extractable with 0.5 M $NaHCO_3$ in the rhizosphere soil $Q(NaHCO_3\text{-}P_i)t = 10^{-5}$ mol

Genotypes	$Q(NaHCO_3\text{-}P_i)_d$ (10^{-6}mol)	$\bar{F}_n$ (10^{-13} mol s^{-1} cm^{-2} root mat area)	Efficiency E (%)
Winter wheat			
Arum	3.7[c]	1.24	37
Foreman	4.4[ab]	1.48	44
Gawain	4.5[ab]	1.51	45
Kosack	3.9[c]	1.31	39
Kraka	4.7[a]	1.58	47
Obelisk	4.3[b]	1.44	43
Pepital	3.8[c]	1.28	38
Sleipner	4.3[b]	1.44	43
Winter barley			
Angora	2.2[c]	0.74	22
Astrid	2.3[c]	0.77	23
Clarine	2.2[c]	0.74	22
Frost	2.8[b]	0.94	28
Hamu	3.5[a]	1.17	35
Marinka	2.5[bc]	0.84	25
Spring barley			
Alexis	2.6[d]	0.87	26
Canut	4.1[a]	1.38	41
Digger	3.2[c]	1.07	32
Etna	3.7[b]	1.24	37
Peel	2.9[cd]	0.97	29
Riga	3.6[b]	1.22	36
Semal	2.8[d]	0.94	28

Means with the same letter are not signifcantly different at 0.05 level of probability using Duncan's Multiple Range Test.

et al., 1989). The nutrients supply to the genotypes was equal (Table 2) indicating that in addition to the nutritional status, root exudation may also depend on plant genetics.

The extension of effective volume of soil supplying P near root surface depends on root hair length (Hendriks et al., 1981; Lewis and Quirk, 1967) and mycorrhiza (Li et al., 1991). The results of present investigation do not directly allow to separate the effect of root hairs from the effect of other mechanisms except rhizosphere pH. Even then, the effect of mycorrhiza seems unlikely because of short experimental period (14 days) and the observed pattern and relatively smaller uniform extension of P depletion profiles, which in case of mycorrhizal infection would probably extend much further (Joner et al., 1995). The variation in extension of depletion profiles only close to the root mat surface suggests the variation in root hair length of wheat genotypes.

The change in diffusion conditions close to roots may affect P uptake kinetic parameters (Nielsen, 1983) and thereby influence the mean net influx ($\bar{F}_n$) into roots. The kinetic uptake parameters of the genotypes investigated are not yet known.

However, the values of $\bar{F}_n$ in Table 4 are close to that of the cereal genotypes investigated by Nielsen and

Schjørring (1983) under field conditions, of moderate P deficiency, if we consider that $NaHCO_3$-P_i makes 54–60% the total P depleted (Gahoonia and Nielsen, 1992a).

Gourley et al. (1994) proposed that germplasms can be described to differ in P efficiency only when similar yields are obtained. In our experiments the relative growth rates of the genotypes did not differ (Table 2) and the spring barley genotypes Etna and Riga originating from the same parental germplasm did not differ in P depletion profiles (Fig. 4); supporting that the observed variation in P depletion may be ascribed to the ability of the germplasms to acquire P from the rhizosphere soil. The present investigation was carried out under controlled conditions in a single environment. The results showed significant variation in their efficiency to acquire P from the rhizosphere soil even with unchanged rhizosphere pH. From the observed patterns of depletion profiles, there seems to be genetic variation in root hair formation and root exudation among the cereal genotypes and these factors appear to play significant role in acquisition of soil phosphorus. Further investigations will be needed to obtain more information on the role of these factors.

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References

Baligar V C and Duncan R R 1990 Crop as Enhancers of Nutrients Use. Academic Press, San Diego, USA.

Bar-Yosef B 1991 Root excretions and their environmental effects: influence on availability of phosphorus. *In* Plant roots: The Hidden Half. Eds. Y Waisel, A Eshel and U Kafkafi. pp 529–557. Marcel Dekker, Inc., New York, USA.

Batten G D 1992 A review of phosphorus efficiency in wheat. Plant and Soil 146, 163–168.

Caradus J R 1994 Selection for improved adaptation of white clover to low phosphorus and acid soils. Euphytica 77, 243–250.

Earl K D, Syers J K and McLaughlln J R 1979 Origin of the effect of citrate, tartrate and acetate on phosphate sorption by soils and synthetic gels. Soil Sci. Soc. Am. J. 43, 674–678.

Elliot Cr C and Läuchi A 1985 Phosphorus efficiency and phosphate-iron interactions in maize. Agron. J. 77, 399–403.

Föhse D and Jungk A 1983 Influence of phosphate and nitrate supply on the root hair formation of rape, spinach and tomato plants. Plant and Soil 74, 359–368.

Föhse D, Claassen N and Jungk A 1991. Phosphorus efficiency of plants. II. Significance of root radius, root hairs and cation anion balance for phosphorus influx in seven plant species. Plant and Soil 123, 261–272.

Gahoonia T S and Nielsen N E 1991 A method to study rhizosphere processes in thin soil layers of different proximity to roots. Plant and Soil 135, 143–146.

Gahoonia T S and Nielsen N E 1992 Control of pH at root-soil interface. Plant and Soil 140, 49–54.

Gahoonia T S and Nielsen N E 1992a The root induced pH change on the depletion of inorganic and organic phosphorus in the rhizosphere. Plant and Soil 143, 183–189.

Gahoonia T S, Claassen N and Jungk A 1992 Mobilization of phosphate in different soils by ryegrass supplied with ammonium and nitrate. Plant and Soil 143, 241–248.

Gahoonia T S, Raza S and Nielsen N E 1994 Phosphorus depletion in the rhizosphere as influenced by soil moisture. Plant and Soil 159, 231–218.

Gerloff G C and Gabelmann W H 1983 Genetic basis of inorganic plant nutrition. *In* Encyclopaedia of Plant Physiology. Eds. A Läuchli and R L Bieleski. pp 453–480. New series Vol. 15b. Springer Verlag, New York, USA.

Gollany H T and Schumacher T E 1993 Combined use of calorimetric and microelectrode methods for evaluating rhizosphere pH. Plant and Soil 154, 151–159.

Gourley C J P, Allan D L and Russelle M P 1994 Plant nutrient efficiency: A comparison of definitions and suggested improvements. Plant and Soil 158, 29–37.

Graham R D 1984 Breeding characteristics in cereals. *In* Advances in Plant Nutrition, Vol. 1. Eds. P B Tinker and A Läuchli. pp 57–90. Praeger, New York, USA.

Grinstad M J, Hedley M J, White R E and Nye P H 1982 Plant induced changes in the rhizosphere of rape seedlings. I. pH change and increase in concentration of soil solution. New Phytol. 91, 19–29.

Hendriks L, Claassen N and Jungk A 1981 Phosphatverarmung des wurzelnahen Bodens und Phosphataufnahme von Maiz and Raps. Z. Pflanzenernähr. Bodenkd. 144, 468–499.

Hoffland E, Findenegg G R and Nelemans J A 1989 Solubilization of rock phosphate by rape. Evaluation of the role uptake pattern. Plant and Soil 113, 155–169.

Joner E J, Magid J, Gahoonia T S and Jakobsen I 1995 Phosphorus depletion and activity of phosphatases in the rhizosphere of mycorrhizal and non-mycorrhizal cucumber (*Cucumis sativus* L.) Soil Biol. Biochem. 27, 1145–1151.

Jones D L and Darrah P R 1994 Role of root derived organic acids in the mobilization of nutrients from the rhizosphere. Plant and Soil 166, 247–257.

Lewis D H and Quirk J P 1967 Phosphate diffusion in soil and uptake by plants. III. ^{31}P movement and uptake by plants as indicated by ^{32}P autoradiography. Plant and Soil 27, 445–453.

Li X L, George E and Marschner H 1991 Phosphorus depletion and pH decrease at the root-soil and hypae-soil interfaces of VA mycorrhizal white clover fertilized with ammonium. New Phytol. 119, 397–404.

Mahon D J 1983 Limitations to the use of physiological variability in plant breeding. Can. J. Plant Sci. 63, 11–21.

Marschner H 1995 Mineral Nutrition in Higher Plants. Academic Press (London) Ltd., London, UK.

Moorby H, Nye P H and White R E 1985 The influence of nitrate nutrition on H-ions efflux by young rape plants (*Brassica napus* var. Emerald). Plant and Soil 84, 403–415.

Møller-Nielsen J and Friis-Nielsen B 1976 Evaluation and control of nutritional status of cereals. Pure-effect of a nutrient. Plant and Soil 45, 339–351.

Murphy J and Riley J P 1962 A modified single solution method for determination of phosphate in natural waters. Anal. Chem. 27, 31–36.

Nagarajah S, Posner A M and Quirk J P 1968 Desorption of phosphate from kaolinite by citrate and carbonate. Soil Sci. Soc. Am. Proc. 32, 507–510.

Nielsen N E 1979 Plant factors determining the efficiency of nutrient uptake from soils. Acta Agric. Scand. 29, 81–84.

Nielsen N E 1983 Plant parameters controlling the efficiency of nutrients uptake from soil. *In* Efficient use of Fertilizers in Agriculture. Proceedings of the Symposium on the research into Agrotechnical Methods aiming at Increasing the Productivity of Crops, Geneva, Switzerland.

Nielsen N E and Barber S A 1978 Differences among genotypes of corn in the kinetics of P uptake. Agron. J. 70, 695–698.

Nielsen N E and Schjørring J K 1983 efficiency and kinetics of phosphorus uptake from soil by various barley genotypes. *In* Genetic Aspects of Plant Nutrition. Eds. M R Saric and B C Loughman. pp 145–150. Martinus Nijhoff, The Hague, the Netherlands.

Noordwijk van M, Willigen de P, Ehlert P A I and Chardon W J 1990 A simple model of P uptake by crops as a possible basis for P fertilizer recommendations. Neth. J. Agri. Sci. 38, 317–332

O'Toole J C and Bland W L 1987 Genotypic variations in Crop plant systems. *In* Advances in Agronomy. Vol. 41. Ed. N C Brady. pp 91–140. Academic Press, Inc., San Diego, USA.

Silberbush M Shomer-Ilan A and Waisel Y 1981 Roots surface phosphatase activity in ecophytes of *Aegilops peregrina*. Physiol. Plant. 53, 501–504.

Schjørring J K and Nielsen N E 1987 Root length and phosphate uptake by barley cultivars grown under moderate deficiency of phosphorus in field experiments. J. Plant Nutr. 10, 1289–1295.

Schjørring J K 1986 Nitrate and ammonium absorption by plants growing at a sufficient or insufficient levels of phosphorus in nutrient solutions. Plant and Soil 91, 313–318.

Wild A, Jones L H P and Mucduff H 1987 Uptake of mineral nutrients and crop growth: The use of flowing nutrient solutions. *In* Advances in Agronomy. Vol. 41 Ed. N C Brady. pp 171–216. Academic Press, Inc., San Diego, USA.

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