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Root hairs and phosphorus acquisition of wheat and barley cultivars

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Abstract

Root-soil contact is an important factor for uptake of a less mobile soil nutrient such as phosphorus (P) by crop plants. Root hairs can substantially increase root-soil contact. Identification of crop cultivars with more and longer root hairs can, therefore, be useful for increasing P uptake in low input agriculture. We studied the root hairs of wheat (*Triticum aestivum* L. cvs. Kosack, Foreman, Kraka) and barley cultivars (*Hordeum vulgare* L. cvs. Angora, Hamu, Alexis, Canut) in relation to P depletion from the rhizosphere in three soils of different P levels (0.45, 1.1 and 1.6 mmoles P kg^{-1} soil; extracted with 0.5 *M* $NaHCO_3$). Root hairs were measured in solution culture having nutrients and concentration similar to soil solution. Root hairs of Kraka were much longer (1.27 $\pm$ 0.26 mm) and denser (38 $\pm$ 3) hairs mm^{-1} root) than those of Kosack which had shorter (0.49 $\pm$ 0.2 mm) and fewer (24 $\pm$ 3) hairs mm^{-1} root) root hairs. Root hairs increased root surface area (RSA) of Kraka by 341%. The increase with Foreman was 142% and with Kosack it was 95%. For winter barley, the length (1.1 $\pm$ 0.3 mm) and density (30 $\pm$ 1 hairs mm^{-1} root) of root hairs of Hamu differed from root hair length (0.52 $\pm$ 0.18 mm) and density (27 $\pm$ 1 hairs mm^{-1} root) of Angora. Root hairs of spring barley cultivars differed in length (Canut 1.0 $\pm$ 0.24 mm; Alexis 0.64 $\pm$ 0.19 mm) but not in density (Canut 31 $\pm$ 1, Alexis 30 $\pm$ 2 hairs mm^{-1} root). Root hair diameter (12 $\pm$ 1μm) did not differ among the cultivars. Root hairs increased RSA of Canut by 245%, Hamu by 237%, Alexis by 143% and Angora 112%. The variation in root hair parameters of the cultivars was related to quantity of P depleted from rhizosphere. The correlation (R^2) between the root hair lengths of wheat cultivars and the quantity of P depleted from the rhizosphere soil (Q) was (0.99^{***}) in low-P, (0.85^{***}) in medium-P and (0.78^{**}) in high-P soil. The values of (R^2) between the root hair surface areas of wheat cultivars and Q were (1.00^{***}) in low-P, (0.74^{**}) in medium-P and (0.66^{**}) in high-P soil. Similar high values of R^2 were found for barley. These results show that the variation in root hairs of cereal cultivars can be considerable and it can play a significant role in P acquisition, especially in low-P soils.

Introduction

Root growth, leading to increased root-soil contact, is an important factor determining the uptake of less mobile nutrients such as phosphorus in soils (Schj orring and Nielsen, 1987). Root hairs increase root-soil contact at low carbon cost (Clarkson, 1991). Selection for root hairs may be a feasible option for improving P acquisition of crop plants (Caradus, 1994). Root hairs are believed to absorb nutrients (Föhse et al., 1991; Itoh and Barber, 1983 a) and water (Cailloux, 1972). Root hairs can exploit soil in the immediate vicinity of the root surface more effectively due to their geometrical arrangement on roots, and ability to increase root surface area (Claassen, 1990). Previous studies (Föhse et al., 1991; Itoh and Barber 1983a) have shown the importance of root hairs in P uptake differences between plant species. Little is known about whether variation in root hair formation exits between cereal genotypes. Recently the quantification of root hairs

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parameters has become easier by the use of image analysis (Care, 1995), so the role of root hairs can now be determined more effectively.

The extent of P depletion zone close to roots can be extended by root hair (Bhat et al., 1976; Lewis and Quirk, 1967). Nye (1966) calculated that with densely clustered root hairs, the concentration of diffusion-limited nutrient like P within the root hair cylinder would become effectively uniform, creating a distinct uniform depletion zone near root surface. Phosphorus depletion profiles in the rhizosphere can now be studied (Gahoonia and Nielsen, 1991, 1992) so that the confounding variation due to factors such as nutritional status, rhizosphere pH and soil moisture are reduced. The aim of this study is to find out the extent of variation in root hairs among cereal cultivars and its relation to P depletion in soil near roots.

Material and methods

Three Danish soils of low–P ($NaHCO)_3$ –P_i = 0.45 mmole P kg^{-1} soil; P in soil solution = 3 μM; sand 65%, silt 18%, clay 15% ; organic matter 12 g kg^{-1}, pH 5.6 in 0.01 *M* $CaCl_2$, CEC = 8.4 $cmol_c$ kg^{-1} at pH 7), medium–P ($NaHCO_3$ –P_i =1.1 mmoles P kg^{-1} soil; P in soil solution = 7 μM; sand 52%, silt 18%, clay 20%; organic matter 19 g kg^{-1}, pH 6.3 in 0.01 *M* $CaCl_2$, CEC =17 $cmol_c$ kg^{-1} at pH 7) and high–P ($NaHCO_3$ –P_i =1.6 mmoles P kg^{-1} soil; P in soil solution =10 μM ; sand 72%, silt 14%, clay 13% ; organic matter 24 g kg^{-1}, pH 6.7 = in 0.01 *M* $CaCl_2$, CEC =13 $cmol_c$ kg^{-1} at pH 7) were used. Phosphorus depletion profiles were studied in the rhizosphere of winter wheat cultivars (Kosack Forernan and Kraka); winter barley cultivars (Angora and Hamu) and spring barley cultivars (Alexis and Canut). The cultivars were chosen from a larger set, because they differed widely in P acquisition from rhizosphere soil (Gahoonia and Nielsen, 1996) when rhizosphere soil pH remained unchanged.

The rhizosphere soil samples were obtained using a thin slicing technique (Gahoonia and Nielsen, 1991). Root surface (represented by root mat of 24.6 cm^2) and the test soil columns remained in contact through a nylon screen of 43 μm inner mesh size. Only root hairs penetrated the screen and grew into the test soil columns. After 14 days, the test soil columns were separated, frozen into liquid nitrogen and sliced into 0.2 mm layers using a freezing microtome. Soil samples were analyzed for 0.5 *M* $NaHCO_3$ extractable inorganic P ($NaHCO_3$–P_i) (Olsen and Sommers, 1982) to obtain P depletion profiles. Unplanted soil was also analyzed as a control. To obtain desorption isotherms, one gram of air dried soil was suspended in P–free 0.01 *M* $CaCl_2$ in soil : solution ratios ranging from 1:10 to 1:1000. The suspensions were shaken daily for 0.5 h for 10 days in a dark room. The solution was then separated from the soil by centrifugation and analysed directly for inorganic P. Soil P was also extracted with 0.5 *M* $NaHCO_3$ and analysed. Soil solution was obtained by displacement (Adam, 1974). Phosphorus was measured by the method of Murphy and Riley (1960).

Based on the methods of Gahoonia and Nielsen (1992, 1996) the rhizosphere soil pH and nutrient status of plants and soil moisture (Θ = 0.21) were kept constant, so that data on the role of root hairs in P acquisition was not confounded by interactive factors. The methods provided good agreement (CV 3.5%) between the replicates (Gahoonia and Nielsen, 1991), facilitating to find small differences in P acquisition between the cultivars. Impedance factor (f=1.58 Θ – 0.17) was calculated as described by Barraclough and Tinker (1981). The quantity of $NaHCO_3$–P_i absorbed from the rhizosphere soil was calculated by integrating the area of each respective depletion profile. The profile of Kraka in medium soil was extrapolated to ascertain the P level of unplanted soil. The distinct uniform depletion zone due to root hairs was defined as the distance from root mat where the measured P concentration points on the depletion profiles did not differ significantly ($p < 0.05$).

Determination of root hairs

To measure the root hair parameters, plants were grown in a temperature-controlled glass house in a basic nutrient solution (Table 1) to accurately determine root hair lengths without the associated difficulties of extracting roots from soils. The ionic strength of the solution was similar to that in soil solution of Danish soils (Nielsen, 1984). Its electric conductivity was maintained at 0.63 mS cm^{-1} by addition of maintenance solution (Table 1) according to a pre-determined relationship between volume added and electric conductivity. The pH was maintained at 5.5 $\pm$ 0.2 by addition of ammonium or nitrate solutions (Gaboonia and Nielsen, 1992). Root systems were harvested for root hair analysis after 7 and 14 days. The roots were placed in a film of water in a microscope slide with raised sides. Root hair images were captured using a video camera fitted to a micro-

Table 1. The composition and concentration of basic (Bc) and maintenance (Mt) solution

Nutrients	N		P	S	K	Ca	Mg	Cl	Na	Fe	Mn	Zn	Cu	B	Mo
	NO_3	NH_4													
					(m*M*)								(*μM*)		
Bc	5.0	0.0	0.05	0.44	0.58	1.92	0.78	0.10	0.00	50	7.0	0.7	0.7	2.0	0.7
Mt	13	3.2	0.54	0.61	7.16	1.40	0.35	0.40	0.24	15	12	6.0	0.9	4.6	0.2

Table 2. Root hair parameters and their impact on root surface area of cereal cultivars. Root hair diameter of all the cultivars was D_h, =12 ± 1 μm. (mean ± st.dev., n = 126)

Genotype	Root hair length (mm) ζ	Number mm^{-1} root n	Total length of hairs mm^{-1} root (mm) $L_h=\zeta$ x n	Surface area (SA) hairs on mm^{-1} root (mm^2) π D_h L_h	Root diameter (mm) D_r	Increased SA mm^{-1} root due to hairs π D_h L_h/π D_r
Winter wheat						
Kraka	1.27±0.26	38±3	48	1.81	0.17±0.04	3.41
Foreman	0.74±0.25	25±2	19	0.71	0.16±0.05	1.42
Kosack	0.49±0.20	24±3	12	0.45	0.15±0.03	0.95
Winter barley						
Hamu	1.10±0.30	30±2	33	1.26	0.17±0.03	2.37
Angora	0.52±0.18	27±1	14	0.53	0.15±0.04	1.12
Spring barley						
Canut	1.00±0.24	31±1	31	1.15	0.15±0.02	2.45
Alexis	0.64±0.19	30±2	19	0.72	0.16±0.05	1.43

scope interfaced with a computer image-grabber board. The images were captured from the main root axis, first order and second order roots of each cultivar grown in three replicates. Root hairs and root parameters were measured by recalling the images using *Video Pro 32* software. The length and density (number mm^{-1} root length) of root hairs as well as the diameter of roots (with measured root hairs) were averaged. The volume of soil (V) exploited by root hair cylinder of a cultivar was calculated as

$$V = \pi[(\zeta)^2 + 2\zeta D_r] \quad (1)$$

where ζ is average root hair length and D_r is average root diameter in Table 2.

Statistical analyses were done using Statistical Analysis System (SAS Institute, 1989). Duncan test was used to determine significance differences between cultivars.

Results

The root hair diameter (12 ± 1 μm) did not differ among the cultivars of wheat and barley. The root hairs of wheat cultivar Kraka were 2.6 times longer and 1.6 times denser than Kosack, resulting in 4 times greater surface area of root hairs (Table 2). This increased root surface area (RSA) of Kraka by 341%, Foreman by 142% and by 95% with Kosack compared to RSA without hairs. Barley cultivars differed mainly in root hair lengths and only slightly in density. Hamu had root hairs 2.1 times longer than Angora, resulting in 2.4 times greater surface area of root hairs (Table 2). Root hairs increased the RSA was by 237% for Hamu and by 112% for Angora. The length of root hairs of Canut was 1.6 times greater than Alexis (Table 2). The increase in RSA due to hairs was 245% for Canut and 143% for Alexis.

The pattern of P depletion profiles in the rhizosphere of wheat cultivars differed (Figure 1). Significant ($p < 0.05$) variation persisted at all the three P

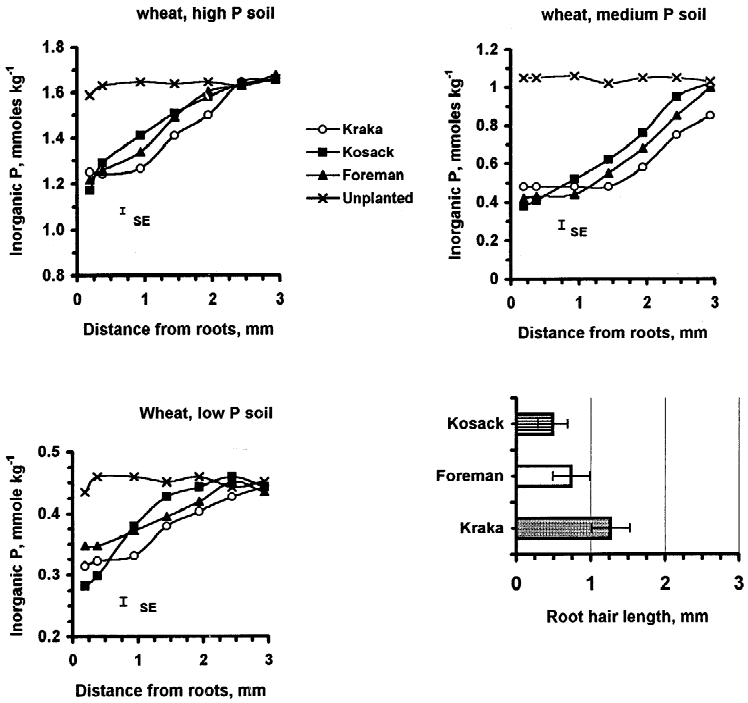

Figure 1. Depletion profiles of phosphorus (extracted with 0.5 *M* $NaHCO_3$) near the roots in three soils of varying P level and the root hair lengths of winter wheat.

levels, though it became less at the highest P level. In medium-P soil, the concentration of soil P within 1.5 mm from the root mat of Kraka did not differ (p <0.05) significantly, showing a distinct uniform depletion zone. In contrast, the depletion profile of Kosack was steep without such distinct uniform depletion zone. The extension of distinct uniform P depletion zones in soil near roots corresponded to the root hair lengths of the wheat cultivars Kraka and Foreman (Figure 1). Kraka absorbed 33% more P in low-P soil (A), 20% more in medium-P soil (B) and 25% more P in high-P soil (C) than Kosack (Table 3).

The barley cultivars also differed significantly (p < 0.05) in the pattern of P depletion profiles in the rhizosphere (Figures 2 and 3). The variation persisted at all three P levels. It became less at the highest P level. However, the district uniform depletion zones as observed with wheat were less clear with barley. Hamu absorbed 66% more P at low P level, 59% more P in medium and 10% more P at the high P level than Angora (Table 3). Canut absorbed 64% more P in low P soil, 60% more P at medium P and 7% more P at the high P level than Alexis. The relative difference in quantity of P depleted between cultivars decreased with increase in P level (Table 3). The length (Table 3) and the surface area of root hairs (Figure 4) were significantly correlated to the quantity of P depleted from the rhizosphere. The correlation was higher in low-P soil than high-P soil, showing the greater importance of root hairs in low-P soils. The difference in degree of depletion (difference of P concentration in unplanted soil and at root surface) was reduced in high and medium P soils as compared to that in low P soil for most of the cultivars.

If we translate the average root hair lengths (Table 2) to cylindrical dimensions in soil (root hair cylinder as calculated by equation 1), Kraka would exploit 5.3 times more soil volume than Kosack, Hamu 3.8 times more than Angora and Canut 2.1 times more than Alexis. This, in addition to uptake of diffusion limited nutrients, may also have consequences for water uptake.

Discussion

The cereal cultivars differed widely in root hair formation (Table 2). Root hair parameters were studied

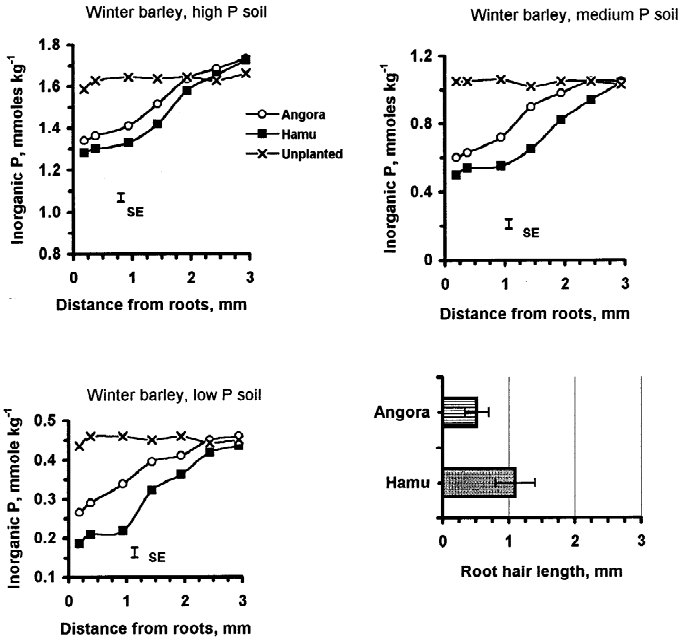

Figure 2. Depletion profiles of phosphorus (extracted with 0.5 *M* $NaHCO_3$) near the roots in three soils of varying P level and the root hair lengths of winter barley.

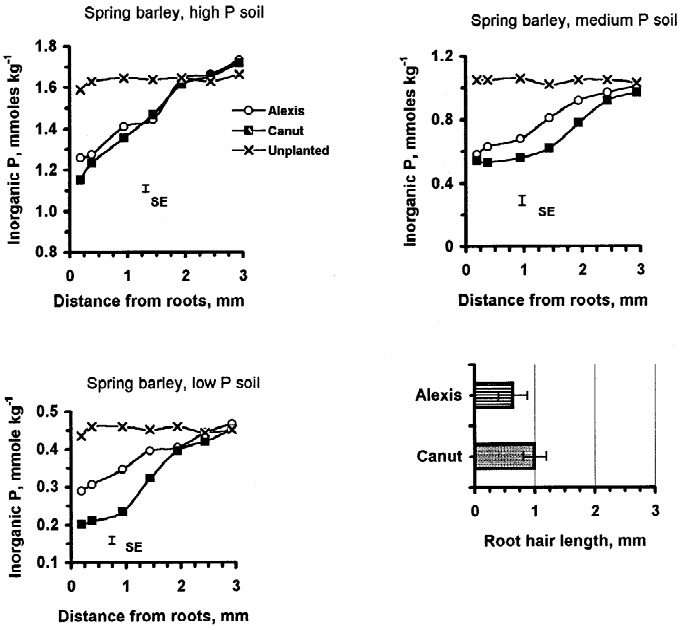

Figure 3. Depletion profiles of phosphorus (extracted with 0.5 *M* $NaHCO_3$) near the roots in three soils of varying P level and the root hair lengths of spring barley.

using solution culture, so that undamaged root hairs were available for measurements using image analysis. Root hairs washed out of soils have been measured for many plant species (Föhse et al., 1991; Itoh and Barber, 1983a). For our study, the removal of entire soil from rhizosheath without damaging the root hairs was not

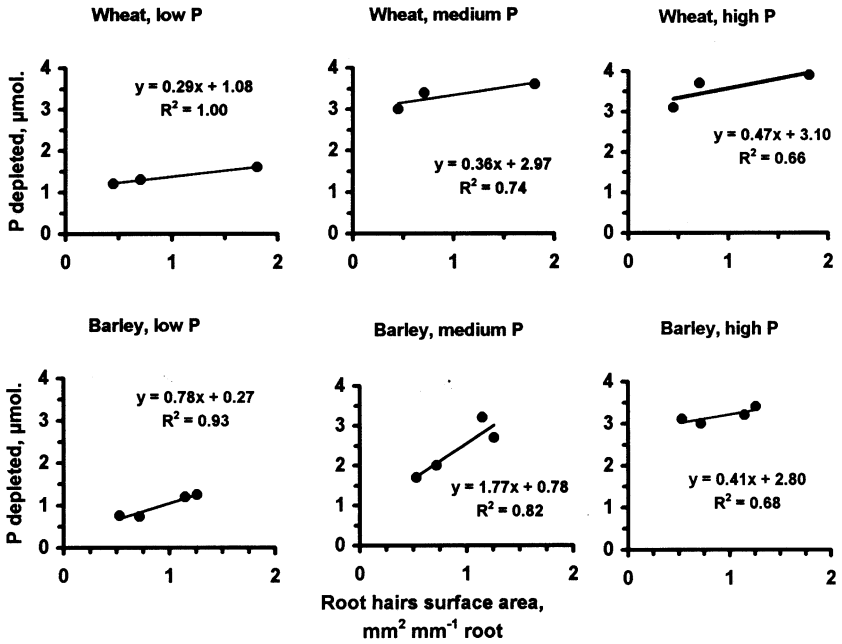

Figure 4. Relationship between surface area of root hairs and the quantity of phosphorus depleted (extractable with 0.5 *M* $NaHCO_3$) from rhizosphere soil by wheat and barley cultivars.

Table 3. Quantities of phosphorus absorbed by cereal cultivar from rhizosphere soil (0 to 3 mm soil one close to the root mats) in three soils of different P levels (A = 0.45, B = 1.1 and C = 1.6 mmoles P kg^{-1} soil) and its correlation (R^2) to root hair lengths

Cultivar	P absorbed (10^{-6} moles)		
	Soil A	Soil B	Soil C
Winter wheat			
Kraka	1.6^{a}	3.6^{a}	3.9^{a}
Foreman	1.3^{b}	3.4^{b}	3.7^{ab}
Kosack	1.2^{b}	3.0^{c}	3.1^{c}
Winter barley			
Hamu	1.25^{a}	2.7^{a}	3.4^{a}
Angora	0.75^{b}	1.7^{b}	3.1^{b}
Spring barley			
Canut	1.20^{a}	3.2^{a}	3.2^{a}
Alexis	0.73^{b}	2.0^{b}	3.0^{ab}
Correlation (R^2) between root hair length and P absorbed			
Wheat	0.99^{***}	0.85^{***}	0.78^{**}
Barley	0.95^{***}	0.81^{***}	0.72^{**}

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

possible even with the use of chemical solutions like 0.27% sodium polyphosphate or 3% HC1. This may be due to strong adhesion of soil in the rhizosheath of grasses (McCully, 1995; Watt et al., 1993). In this study we assumed that genetic differences in root hair formation should remain comparable in solution culture. It is accepted that root hairs may behave differently in soils (Claassen, 1990). According to Mackey and Barber (1984) root hairs may be shorter in solution culture than in soils.

The experimental approach applied in this study ensured constant root surface area, rhizosphere soil pH, nutritional status of plants (Gahoonia and Nielsen, 1992, 1996) and soil moisture (Gahoonia et al., 1994), so that the role of root hairs in P acquisition could be assessed without their confounding effects. It was found that the root hairs differences among cereal cultivars affected acquisition of P from rhizosphere soil. The cultivar differences may explain why root hairs of wheat in other studies were short and not contributed to P uptake (Itoh and Barber, 1983a).

Whether root hairs affect uptake of a nutrient depends on the relation between root hair length and the magnitude of the effective diffusion coefficient (De) in soil (Barber and Silberbrush, 1984). Root hairs can be important for uptake of nutrients having De of 1×10^{-9}

cm^{-2} s^{-1} or less (Itoh and Barber, 1983b). From the desorption isotherm of the medium P soil, we estimated buffer power (b = 357) from the change in $NaHCO_3$–P; concentration (ΔC = 500 μmoles kg^{-1} soil in most depletion profiles) and the corresponding change in concentration of P in equilibrium solution (Δc =1.4 μM), giving the value of De = 8.4×10^{-10} cm^{-2} s^{-1}.

$$\Delta x = (2De.t)^{\frac{1}{2}} \quad (2)$$

Δ x = mean diffusion distance (cm), t = time (s)
According to Equation 2 (Jost, 1952), at this value of De, phosphorus will diffuse to up to 0.45 mm during the experimental period (14 days). This distance is close to the root hair lengths of Kosack (Table 2). This may explain why Kosack showed no distinct uniform P depletion close to the roots (Figure 1).

Smaller differences in degree of P depletion at higher P levels may be due to the increased P transport from bulk soil towards the root surface (Nye, 1966) or a decrease in root hair lengths with higher solution P (Föhse and Jungk, 1983). Other physiological mechanisms such as root exudates may also influence soil P acquisition (Jones and Darrah, 1994). Root exudation depends on nutritional status of plants (Hoffland et al., 1989), which was kept constant. Therefore, we assume that the role of root exudation, unless it is genetically controlled, should be of minor importance in this study. High correlation between root hair parameters and the quantity of P depleted from rhizosphere emphasizes the significance of root hairs in soil P acquisition (Table 3, Figure 4).

The significance of root hairs, in P acquisition may be reduced if they are short and develop in the pre-existing depletion soil zone caused by the absorption of ions by epidermal cells prior to root hair initiation (Clarkson, 1991). But rather long root hairs of cereals may intercept P diffusing towards the roots at some distance. When the root hairs are shorter there may be more mycorrhizal infection (Baon et al., 1994). Microscopic examination of the root mats in rhizosphere soil studies did not show the presence of mycorrhizal hyphae.

The wide variation in root hairs formation and its relation to the soil P acquisition suggests that the acquisition of soil inorganic P may be increased by selection of cultivars for longer and denser root hairs. Whether the root hair characteristics are heritable, remains to be investigated. Studies with white clover (Caradus, 1979) reported that heritability for root hair length among white clover genotypes ranged from 0.33 – 0.44. More studies on the parents of the cereal cultivars in various environments will reveal information on the heritability of root hairs; and on the feasibility of selection for root hairs to improve P acquisition from soils. In moist and well P fertilized soils with soil: solution concentration above 8 μM P, transport of P through soils may not be a rate-limiting factor (Barraclough, 1986). The desired reduction in P fertilization in future low-input agriculture may lead to lower P in soil solution. Under these conditions, P transport in soils may become increasingly limiting for P uptake. The selection for longer root hairs may help to lessen the effect of such limitation.

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