Plant and Soil 86, 321–331 (1985). Ms. 6143

Effect of soil moisture and phosphate level on root hair growth of corn roots*

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Received 23 October 1984. Revised January 1985

Key words Root hair density Root hair length Root length Soil P level Soil moisture *Zea mays* L.

Summary Root hairs have been shown to enhance P uptake by plants growing in low P soil. Little is known of the factors controlling root hair growth. The objective of this study was to investigate the influence of soil moisture and P level on root hair growth of corn (*Zea mays* L.). The effect of volumetric soil moistures of 22% (M_0), 27% (M_1), and 32% (M_2) and soil (Raub silt loam, Aquic Argiudoll) P levels of, 0.81 (P_0), 12.1 (P_1), 21.6 (P_2), 48.7 (P_3), and 203.3 (P_4) μmol P L^{-1} initially in the soil solution, on shoot and root growth, P uptake, and root hair growth of corn was studied in a series of pot experiments in a controlled climate chamber. Root hair growth was affected more by soil moisture than soil P. The percentage of total root length with root hairs and the density and length of root hairs on the root sections having root hairs all increased as soil moisture was reduced from M_2 to M_0. No relationship was found between root hair length and soil P. Density of root hairs, however, was found to decrease with an increase in soil P. No correlation was found between root hair growth parameters and plant P content, further suggesting P plays a secondary role to moisture in regulating root hair growth in soils. The increase in root hair growth appears to be a response by the plant to stress as yield and P uptake by corn grown at M_0 were only 0.47 to 0.82, and 0.34 to 0.74, respectively, of that measured at M_1 across the five soil P levels. The increase in root hair growth at M_0, which represents an increase of 2.76 to 4.03 in root surface area, could offset, in part, the reduced rate of root growth, which was the primary reason for reduced P uptake under limited soil moisture conditions.

Introduction

Barley and Rovira[1] were the first to obtain conclusive evidence that root hairs enhance phosphorous, P, uptake. In a 3-day study, they found root hairs of pea (*Pisum sativum* L.) seedlings increased P uptake by 78%. A number of workers[3,6,12,15,25], using autoradiographs, have obtained indirect evidence showing that root hairs enhance P uptake. In these studies, the depletion zone for P around the root surface corresponded closely to the length of the root hair. In comparing three populations of white clover (*Trifolium repens* L.), which differed in root hair length, Caradus[8] found yield and P content of clover grown in low-P soil increased as root hair length increased. Itoh and Barber[13] found the

* Journal Paper No. 10,066 Purdue Univ. Agric. Exp. Stn., W. Lafayette, IN 47907. Contribution from the Dep. of Agron. This paper was supported in part by a grant from the Tennessee Valley Authority.

root hairs of three of six plant species studied contributed significantly to P uptake. The length and to a lesser extent the density of root hairs (no. per cm of root) appeared to determine the extent to which P uptake was enhanced. In a subsequent study, Itoh and Barber[14], using a simulation model, found changes in root hair length had the greatest effect on calculated P uptake.

Plant species differ in both their length and density of root hairs. Dittmer[10] investigated 34 species and found root hair length varied from 0.08 to 1.5 mm, with most less than 0.5 mm. Caradus[7] found root hair length to vary from 0.4 to 1.01 mm with 10 grass and 0.17 to 0.29 mm, with 11 legume species. Itoh and Barber[13] found differences in both length (0.04 to 0.6 mm), and density (560 to 1819 cm^{-1}) of root hairs on roots of six contrasting plant species. Investigations of nutritional factors controlling root hair growth have frequently been with solution culture studies[11,24]. The effect of soil factors on root hair growth has been restricted to a limited number of studies[1,3,4,19]. The interaction of soil moisture and P level on root hair growth of corn (*Zea mays* L.) has not been investigated. An understanding of this interaction may explain why the simulation model of Claassen and Barber[9], which does not consider the contribution made by root hairs when calculating P uptake, underpredicts P uptake by corn (*Zea mays* L.) grown under limited soil moisture conditions[16] and with soils of low P[21]. The objective of this study was to investigate the interaction of soil moisture and P level on root hair growth on corn roots.

Materials and methods

Soil moisture and phosphate levels

The soil used, Raub silt loam (Aquic Argiudoll) with 3 P levels, was collected from long-term fertility plots at the Purdue Agronomy Farm, Lafayette, IN., that had been receiving an average of 0 (P_0), 22 (P_1), and 44 (P_2) kg P ha^{-1} y^{-1} for 30 years. No P had been applied in the year prior to sampling. The P_1 soil had not received potassium, K, during this period, while the P_0 and P_2 soil had both received an average of 40 kg K ha^{-1} y^{-1}. In addition to these 3 P levels, extra P_0 soil was collected to which 200 (P_3) and 350 (P_4) mg P as $Ca(H_2PO_4)_2$ kg^{-1} of soil was added. The soils were heated moist at 70°C for 5 days, and then incubated at 25°C for a further 20 days to facilitate rapid equilibration of added P[2]. All soils were kept moist and, before potting, passed through a 6-mm sieve.

Table 1 gives the pH, at a soil:solution ratio of 1:2.5; Bray P_1[5] at soil:solution ratio of 1:10; C_{li}, initial concentration of P in the soil solution before the start of plant growth[23]; b, the buffer power; $\Delta C_s/\Delta C_{li}$ where C_s is the P concentration on exchange sites[23]; and exchangeable cations[27] of the soils.

Three soil moisture levels, M_0, M_1, and M_2 representing soil moisture held at water potentials of −173, −33, and −7.5 kPa, respectively were used. At a bulk density of 1.2 Mg m^{-3} these are volumetric moisture contents of 22% (M_0), 27% (M_1), and 32% (M_2).

Growth conditions

Phosphorus uptake by corn from Raub soil at four of the five P levels (P_1 to P_4) each at 3 moisture levels (M_0, M_1, and M_2) was measured in 3-L pots. With the P_0 soil, corn was only

Table 1. Several chemical characteristics of the Raub silt loam used in the study

Soil P level	pH H_2O	Bray-P_1 (mg kg^{-1})	C_{li}^{1} (μmol P l^{-1})	b^2	Exchangeable K^+ (cmol(p^+) kg^{-1})	Na^+	Ca^{2+}	Mg^{2+}
P_0	6.2	4	0.8	322	0.33	0.02	8.64	2.88
P_1	5.7	55	12.1	134	0.14	0.09	8.34	2.73
P_2	6.3	74	21.6	104	0.53	0.03	10.80	3.40
P_3	6.1	95	48.7	45	0.46	0.02	9.85	3.12
P_4	5.8	129	203.3	18	0.48	0.03	9.82	2.98

[1] C_{li}, initial concentration of P in the soil solution before the start of plant growth.
[2] b, buffer power.

grown at M_1. Soil was packed to a bulk density of 1.2 Mg m^{-3}. The gravametric moisture content of the soils was close to 17.5%, at potting. Corn cv. Pioneer 3369A, was used. Seeds were germinated between wet rolled paper towels. After 7 d, uniform plants were selected, roots were trimmed to 4-cm length to provide branching and the plants were transferred to the soil. Four corn plants were transplanted into each pot and moisture was adjusted to the desired levels. Corn was grown in a controlled-climate chamber with a 16-h illumination of 450 μmol m^{-2} s^{-1} at plant level at 25°C. The soil surface was covered with black polyethylene film, and air in the chamber was maintained above 90% relative humidity, to minimize water loss. Pots were watered twice daily by weight. Each treatment had two replicates. Plants were harvested after 14 d (21 d from germination).

Corn shoots were removed and soil moisture contents were determined on each pot by taking 2-cm diameter cores in 2-cm depth increments to the bottom of the pot (12 cm). A check on soil moistures with the P_2 soil was also made at 7 d. Average volumetric moisture contents for the P_2 soil for samples taken at 5 depths at 7 and 14 d were 22.21 ± 0.56% at M_0, 26.33 ± 0.82% at M_1, and 32.53 ± 1.07% at M_2.

Measurement of corn root and root hair growth

After removing corn shoots, most of the roots were picked by hand from the soil, then the remaining roots were collected by washing the soil through a 0.3 mm opening sieve. Root length was measured by the line intersect method[26]. Root-fresh weight was used to calculate mean root radius, r_0, from the relationship $(FW_r/L_r\Pi)^{1/2}$ where FW_r is the fresh weight of roots, and L_r, the length of roots in cm.

Root hairs were measured under a microscope. For each plant, approximately 30 1-cm lengths of root were examined. The fraction of root length having root hairs was estimated. Representative root segments with root hairs were photographed. Length, diameter, and density of root hairs were measured from the photographs. No distinction was made between primary and secondary roots in measuring root hair lengths and densities. A preliminary investigation indicated root hair growth was similar on primary and secondary roots. This is consistent with the findings of Shierlaw and Alston[22]. Density of root hairs was calculated by assuming that the root hairs counted on one side of the root represented one quarter of the total. Root hair diameters did not change significantly with either soil moisture or P level. An average diameter (0.012 mm) was used in calculating root hair surface area.

Roots and shoots were dried, weighed, ground and analyzed colormetrically for total P[18], following digestion with sulphuric acid and hydrogen peroxide.

Results

Effect of soil moisture and P level on P uptake

As soil moisture was raised from M_0 to M_1 and soil P level was increased, plant weight and P uptake by corn increased (Table 2). Raising

Table 2. Effect of soil moisture and phosphate level of Raub soil on plant weight (shoot plus roots) and phosphorus uptake by 21-day-old-corn

Soil P level	Plant weight ($g\,pot^{-1}$)			P uptake ($mg\,pot^{-1}$)		
	M_0	M_1	M_2	M_0	M_1	M_2
P_0	–	2.22	–	–	2.78	–
P_1	1.07	1.33	1.26	3.05	4.61	4.53
P_2	1.96	2.39	2.13	5.12	6.89	6.37
P_3	1.24	2.64	2.29	5.18	15.31	13.20
P_4	2.14	3.37	3.24	13.71	26.70	25.65

ANOVA table of F ratios.[2]

Variance	Yield weight	P uptake
Moisture	41.2**	53.2**
Soil P level	117.2**	292.8**
Moisture x soil P level	17.2**	29.5**

[1] Volumetric soil moisture levels, M_0 (22%), M_1 (27%), M_2 (32%).
[2] Analysis of variance does not include P_0 soil.
** Significant at the 0.01 level.

soil moisture from M_0 to M_1 resulted in 1.47- to 1.82-fold increase in plant weight and 1.35- to 2.95-fold increase in P uptake by corn. Increasing P levels from P_0 to P_4 gave a 9.6-fold increase in P uptake by corn grown at M_1. A further soil moisture increase from M_1 to M_2 slightly decreased both plant weight and P uptake (Table 3).

Effect of soil moisture and P level on root growth

Both soil moisture and P level affected corn root growth (Table 3). Excluding the P_1 soil, which had a low K level (Table 1), root surface area of corn grown at M_1 increased ($P < 0.01$) as soil P increased. Root length and surface area at M_1 was greater than at either M_0 or M_2 (Table 3).

Effect of soil moisture and P level on root hair growth

The percentage of total root length with root hairs at each P level decreased as soil moisture was increased (Fig. 1). Under limited soil moisture conditions (M_0), soil P had no effect on the percentage of total root length with root hairs, whereas at M_1 and M_2 the percentage declined as soil P increased (Fig. 1).

The length (Table 4) and density (Fig. 2) of root hairs of corn roots also decreased as soil moisture was increased from M_0 to M_2. A comparison of corn roots grown with the P_1 soil (Fig. 3) illustrates the pronounced effect soil moisture had on both the length and density of root hairs. The relationship between root hair length and soil P

Table 3. Effect of soil moisture and phosphate level of Raub soil on root length and root surface area of 21-day-old corn

Soil P level	Root length (cm pot^{-1}) M_0	M_1	M_2	Root surface area (cm^2 pot^{-1}) M_0	M_1	M_2
P_0		6522			686	
P_1	2232	3572	3084	336	606	572
P_2	5564	8209	7263	437	825	734
P_3	2344	7685	5143	383	1304	905
P_4	3547	7474	6272	602	1455	1261

ANOVA table of F ratios.

Variance	Root length	Root surface area†
Moisture	9.9**	10.3**
Soil P level	11.5**	7.5**
Moisture x soil P level	2.0	2.1

[1] Volumetric soil moisture, M_0 (22%), M_1 (27%), M_2 (32%).
† Analysis of variance does not include P_0 soil.
** Significant at the 0.01 level.

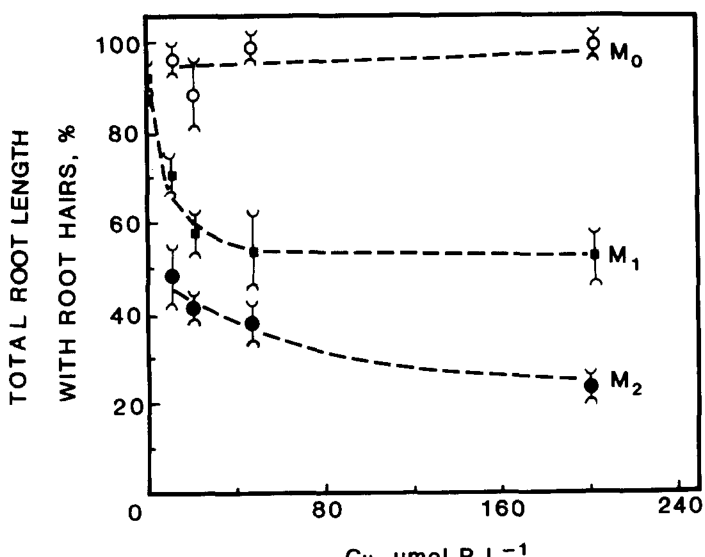

Fig. 1. Change in the percentage of total root length with root hairs of 21-day-old corn plants grown with Raub soil at three moisture (M_0, M_1, and M_2) and five phosphate (P_0, P_2, P_3, and P_4) levels. Standard deviations are represented by *vertical lines* at each data point.

was less well defined (Table 4). The density of root hairs, however, with the exception of the P_1 soil, declined as soil P was raised (Fig. 2). The low level of K in the P_1 soil (Table 1) may explain the reduced density of root hairs at M_0 and M_1 with this soil, when compared to the root

Table 4. Effect of soil moisture and phosphate level on root hair length of 21-day-old corn roots

	Root hair length (mm)		
Soil P level	M_0 [1]	M_1	M_2
P_0		0.253 ± 0.092 [2]	
P_1	0.416 ± 0.091	0.387 ± 0.124	0.262 ± 0.109
P_2	0.288 ± 0.056	0.233 ± 0.029	0.260 ± 0.056
P_3	0.403 ± 0.075	0.333 ± 0.046	0.285 ± 0.056
P_4	0.472 ± 0.076	0.378 ± 0.054	0.213 ± 0.053

[1] Volumetric soil moisture levels, M_0 (22%), M_1 (27%), M_2 (32%).
[2] Standard deviation.

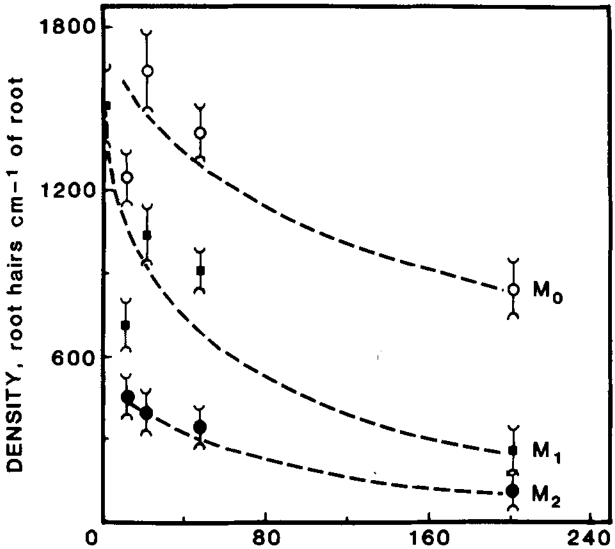

Fig. 2. Change in the density of root hairs per cm of 21-day-old corn root sections having root hairs grown with Raub soil at three moisture (M_0, M_1, and M_2) and five phosphate (P_0, P_1, P_2, P_3, and P_4) levels. Standard deviations are represented by *vertical lines* at each data point.

hair densities with the P_0 and P_2 soil (Fig. 2). No correlation was found between root hair length and the P content of either the root or shoot, even though the P content of the shoot varied from 1.34 to 8.80 g kg^{-1} with the five soil P levels.

Root hairs had a pronounced effect on total root surface area (Fig. 4). Even at high soil P levels, root hairs almost tripled the total root surface area of corn grown at M_0. In contrast under wet soil conditions (M_2) root hairs contributed little to root surface area, even with the P_0 soil (Fig. 4).

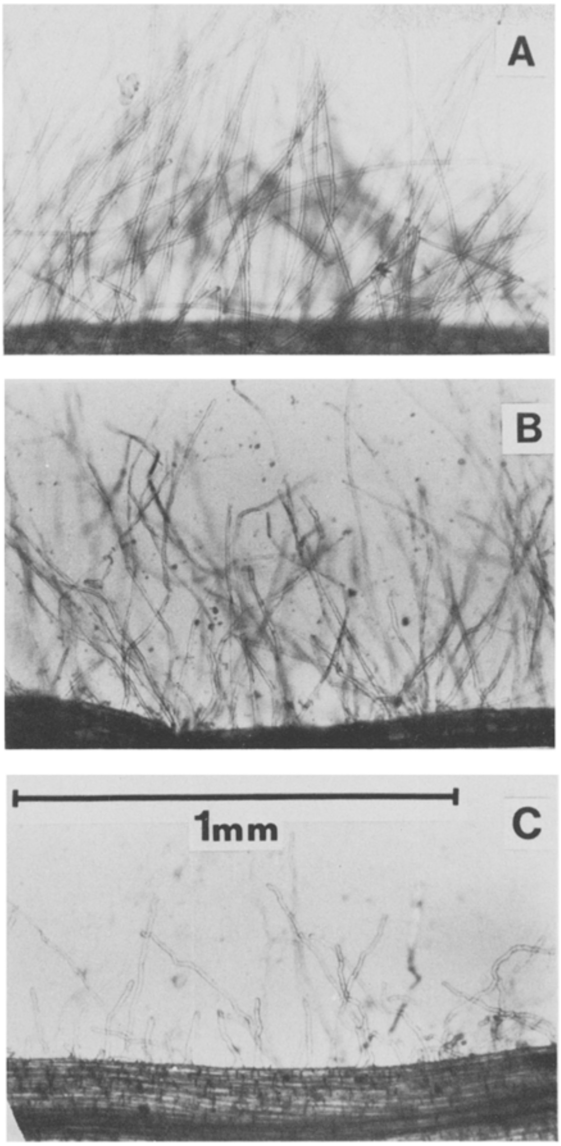

Fig. 3. Microphotographs of root hairs of corn roots, grown with the P_1 soil at volumetric moisture contents of (a) 22%, (b) 27%, (c) 32%.

Discussion

Root hair growth was affected more by changes in soil moisture than changes in soil P. Not only did the percentage of total root length with root hairs increase, as soil moisture decreased, but also the density and length of root hairs increased. Reid and Bowen[19] measured an

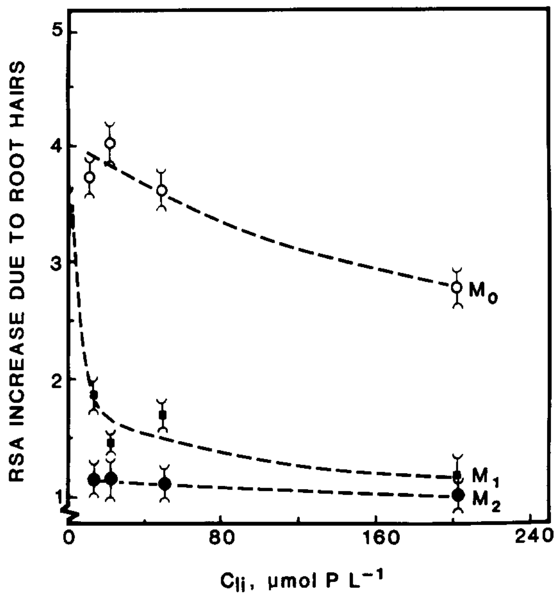

Fig. 4. Increase in root surface area due to root hairs of 21-day-old corn grown with Raub soil at three moisture (M_0, M_1, and M_2) and five phosphate (P_0, P_1, P_2, P_3, and P_4) levels. Increase in root surface area (RSA) due to root hairs was calculated from the equation RSA = $2\Pi L_r r_0 + 2\Pi L_{rh} r_{rh} d_{rh} P_{rh}/2\Pi L_r r_0$ where L_r is the length of roots, r_0 mean root radius, L_{rh} average length of root hairs, r_{rh} mean root hair radius, d_{rh} density of root hairs, and P_{rh} the percentage of total root length with root hairs. Standard deviations are represented by *vertical lines* at each data point.

increase in length of root hairs of 8- to 13-day-old *Medicago truncatula* roots as soil moisture decreased from 22% (– 190 kPa) to 9% (– 1400 kPa). As in this study, Caradus[7], working with legumes and grasses, found no relationship between root hair length and soil P. Bhat and Nye[3], however, observed that root hairs of rape roots were generally longer in low P soil. Foehse and Jungk[11] found root hair length increased in solution culture as P concentration decreased. The decrease in root hair density as soil P increased, of this study, is consistent with the findings of Foehse and Jungk[11] using 3 plant species, but contrasts with that of Bole[4] who found root hair density of several lines of wheat (*Triticum vulgare* L.) to increase as soil P increased.

In addition to finding no correlation between root hair length and soil P, no relationship was found between root hair growth and the P content of corn, even though the P content of the shoot varied from 1.34 to 8.80 g kg^{-1} with the five soil P levels. In contrast, Foehse and Jungk[11] found a correlation between root hair growth of rape (*Brassica napus* L.), spinach (*Spinacea oleracea* L.), and tomato (*Lycopersicon esculentum* M.) and plant P content in a solution culture experiment. They concluded from this that root hair growth is regulated by the P content of the plant and to a lesser extent the P concentration in solution at the root surface. However, with corn grown in soil, P appeared to play a secondary role to moisture in controlling root hair growth.

The length and density of root hairs, which varied from 0.150 to 0.486 mm and 200 to 1600 cm^{-1}, respectively are consistent with those reported by several workers[20,22] for corn. Shierlaw and Alston[22] found the length and density of corn root hairs to vary from 0.516 to 0.558 mm and 550 to 650 cm^{-1}, respectively; in a climate-chamber study. With a sandy loam, Reid[20] found Medicago root hairs as long as 0.9 mm and densities as high as 1616 cm^{-1} in a pot experiment.

The increased growth of root hairs, at M_0, appears to be a response by the plant to stress, as both corn yield and P uptake were less with this treatment (Table 2). In addition to maintaining liquid continuity from the root surface to the soil under limited soil moisture conditions increased root hair growth provides a greater surface area for P diffusion, increasing the supply of P from the soil. Root hairs increased the root surface area of corn grown at M_0 2.8- to 4.0-fold (Fig. 4). This could offset; in part, the reduced rate of corn root growth, which was the primary reason for lower P uptake under limited soil moisture conditions[16]. The extent to which root hairs enhance P uptake, however, depends not only on their length and to a lesser extent density but also on the supply of P, by diffusion, from the soil[14]. As the P diffusion coefficient increases, the effectiveness of root hairs decreases because the P concentration gradient extends out past the root hairs within a few days. Increased root hair growth, under limited soil moisture conditions, with high P soils may therefore contribute little to P uptake.

The pronounced effect of soil moisture on root hair growth explains the results obtained with corn in the field study of Mackay and Barber[17]. In this study, root hair growth was found to increase in the topsoil at two sites over the growing season, even though Bray-P_1 was 49 mg kg^{-1} at one site, and 96 mg kg^{-1} of soil at the other. In contrast, in the subsoil, little change was found in the density and length of root hairs, even though Bray-P_1 was less than 1 mg kg^{-1} of soil. Volumetric moisture contents of the topsoils in the study of Mackay and Barber[17], decreased from 22% to 15% at one site and 27.5 to 19.5% at the other side during the growing season. In contrast, the moisture content of the subsoil remained above 28% at both sites late into the season. The increased bulk density of the subsoil, which was greater than 1.5 Mg m^{-3} at both sites, may also explain, in part, the reduced root hair growth in the subsoil[1]. Generally under field conditions, wetting and drying of the surface soil occurs during the growing season. Because the soil moisture levels were maintained over narrow ranges in this study, it is unclear whether root hairs produced under limited soil moisture conditions persist to enhance P uptake at higher moisture contents, and whether roots initiated under wet conditions produce root hairs when soil moisture level decreases. A knowledge of this relationship would aid in understanding more fully root hair growth under field conditions and in addition aid in evaluating the role played by root hairs in P uptake by plants.

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