

Phosphorus efficiency of plants

II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species

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Abstract

Föhse *et al.* (1988) have shown that P influx per unit root length in seven plant species growing in a low-P soil varied from 0.6×10^{-14} to 4.8×10^{-14} mol cm⁻¹s⁻¹. The objective of this work was to investigate the reasons for these differences. No correlation was found between P influx and root radius, root hairs, cation-anion balance and Ca uptake. However, when root hairs were included in mathematical model calculations, the differences of P influx could be accounted for. These calculations have shown that in soils low in available P, contribution to P uptake by root hairs was up to 90% of total uptake.

The large contribution of root hairs to P uptake was partly due to their surface area, which was similar to that of the root cylinder. However, the main reason for the high P uptake efficiency of root hairs was their small radius (approx. 5×10^{-4} cm) and their perpendicular growth into the soil from the root axis. Because of the small radius compared to root axes, P concentration at root hair surfaces decreased at a slower pace and therefore P influx remained higher. Under these conditions higher I_{\max} (maximum influx) or smaller K_m values (Michaelis constant) increased P influx. The main reasons for differences found in P influx among species were the size of I_{\max} and the number and length of root hairs. In a soil low in available P, plant species having more root hairs were able to satisfy a higher proportion of their P demand required for maximum growth.

Introduction

As shown earlier (Föhse *et al.*, 1988), plant species differ widely in P efficiency. Morphological as well as physiological root properties may influence P uptake from soil. Because of the cylindrical geometry, root radius influences P flux from soil to roots and thus affects influx (Nye, 1966, 1973; Silberbush and Barber, 1983). Root hairs should therefore influence P uptake. Using autoradiography, Bhat and Nye (1974a, b) and Hendriks *et al.* (1981) have shown that the width of the P depletion zone around roots was

increased by root hairs. Itoh and Barber (1983a, b) used a mechanistic model to simulate P uptake by several plant species with different root hair growth. When root hairs were included in their calculations, values of measured and calculated P uptake agreed closely. On the other hand, Bole (1973) found no such relationship between root hairs and P influx of wheat lines differing in root hair length.

Plants can affect P availability also by changing the rhizosphere chemically. Riley and Barber (1971) found that the P concentration of soybean shoots was related to the rhizosphere pH. A

decrease in pH, due to the effect of $\text{NH}_4\text{-N}$ nutrition on cation-anion balance, caused an increase in P concentration in plants. Similar results were reported by Van Ray and van Diest (1979), Nye (1981), Hedley *et al.* (1982), Bekele *et al.* (1983) and Gahoonia (1987).

Van Ray and van Diest (1979) and Bekele *et al.* (1983) postulated that P uptake of some species may be enhanced by Ca uptake. By the principle of mass-action, high Ca uptake causes an increase in P solubility from rock phosphates. Furthermore, plants can increase P solubility in the rhizosphere by exudation of substances which may chelate P sorbents, like Fe and Al compounds. This mechanism was proposed by Gardner *et al.* (1983) and confirmed by Horst and Waschkes (1987). Dinkelaker *et al.* (1989) have shown that white lupin roots exudated large amounts of citric acid and in this way precipitated Ca citrate.

It must therefore be concluded that a number of reasons may contribute to the differences found in P influx among species. The objective of this paper is to quantify the effect of root radius, root hairs and cation-anion balance on P influx of different plant species. In order to integrate various possible factors, mechanistic mathematical models were used for quantitative assessments of the influence of morphological and physiological root properties on P influx.

Materials and methods

Seven plant species (Table 1) were grown in a pot experiment on a subsoil derived from loess with free CaCO_3 , pH (CaCl_2) of 7.7 and a CAL-P concentration of 0.4 mg/100 g soil. Phosphorus application as $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$ was varied from 0 to 80 mg/100 g soil. Two harvests were made in a sequence as shown in Table 1. For more details see Föhse *et al.* (1988).

The P, Ca, K, Mg and Na contents of the shoots were determined after dry-ashing. Total N was determined, after reduction of nitrate, by Kjeldahl. Sulfur and chloride were determined by X-ray fluorescence spectroscopy (Schnug, 1982).

Root hair length and root hair density were measured at the second harvest. A soil core was

Table 1. Plant species, time between sowing and the first and second harvests and the number of plants per pot

Plant species	Time until harvest (days)		Number plants per pot	
	t_1	t_2	1 harvest	2 harvest
Bean <i>Phaseolus vulgaris</i> , var. nanus. cv. Loma	30	40	6	3
Rape <i>Brassica napus</i> , cv. Quinta	28	43	8	4
Wheat <i>Triticum aestivum</i> , cv. Kolibri	23	41	20	10
Spinach <i>Spinacea oleracea</i> , cv. Medania	34	44	8	4
Tomato <i>Lycopersicum esculentum</i> , cv. Eurocross B	49	57	12	6
Ryegrass <i>Lolium perenne</i> cv. Printo	34	50	40	20
Onion <i>Allium cepa</i> , cv. Stuttgarter Riesen	55	69	40	20

taken from each pot, suspended in water and the roots were carefully separated from the soil. The clean roots were suspended in water and photographs taken under a microscope. The photographs were magnified and root hair density and length determined as described by Föhse and Jungk (1983).

Total root length was estimated according to Newman (1966) after separation of the roots from soil by washing. Phosphorus influx was calculated by the formula of Williams (1948)

$$I_n = \frac{U_2 - U_1}{RL_2 - RL_1} \frac{\ln(RL_2/RL_1)}{t_2 - t_1} \quad (1)$$

where $U = \text{P uptake, mol plant}^{-1}$. $RL = \text{root length, cm plant}^{-1}$ and $t = \text{time, s}$. Subscripts 1 and 2 refer to first and second harvest.

Model calculation

Two mechanistic models were used to simulate P uptake from soil. Both models are based on ion transport from soil to the root by mass flow and diffusion, and on Michaelis-Menten uptake kinetics into the root. The first model treated the root as a smooth cylinder, *i.e.* nutrient uptake was assumed to occur only at the surface of the root cylinder (Claassen *et al.*, 1986). The second model included nutrient uptake by root hairs (Claassen, 1990). Soil and plant parameters required for modeling P uptake are listed below.

Soil parameters

C_{ii} : the initial P concentration of the soil solution, mol cm^{-3} . It was measured in the displaced soil solution as proposed by Adams (1974).

b: the buffer power calculated from the ratio of $\Delta C/\Delta C_1$, where ΔC is the amount of P added as fertilizer and ΔC_1 the corresponding increase in C_1 , the concentration in soil solution.

D_e : the effective diffusion coefficient ($\text{cm}^2 \text{s}^{-1}$), was calculated from the formula of Nye (1966)

$$D_e = D_1 \theta f / b \quad (2)$$

where D_1 = diffusion coefficient in water ($0.89 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ for H_2PO_4^- at 25°C), θ = volumetric water content of the soil, $0.26 \text{ cm}^3 \text{ cm}^{-3}$, and f = impedance factor, calculated after Barraclough and Tinker (1981), ($f = 1.58\theta - 0.17$).

Plant parameters

I_{\max} : maximum net influx, $\text{mol cm}^{-2} \text{ s}^{-1}$, was determined from the influx measured at high P application (see Fig. 3 in Föhse *et al.*, 1988). Since I_{\max} is extrapolated for infinite concentration, the measured value was increased by 10%. For example, the maximum measured influx for spinach was $7.27 \times 10^{-14} \text{ mol cm}^{-2} \text{ s}^{-1}$, which results in an I_{\max} value of $7.27 \times 1.10 = 8.00 \times 10^{-14} \text{ mol cm}^{-2} \text{ s}^{-1}$. This is the I_{\max} value

for plants at ample P supply. However, P-deficient plants may develop up to twice as high I_{\max} values (Jungk, 1974). Therefore, I_{\max} of the plants at the lowest P supply was doubled. For the intermediate treatments, I_{\max} was interpolated according to P concentration in the shoot. This procedure is shown for spinach in Table A1 (see Appendix). The I_{\max} values initially determined per cm root length were divided by the root surface area per cm root length to express I_{\max} on a cm^2 basis, as required for calculations in the model. When root hairs were included in this calculation, their surface area was added to the area of the root cylinder.

C_{imin} : soil solution concentration (mol cm^{-3}) at which net influx equals zero. As shown before (Föhse *et al.*, 1988), influx was almost nil in the unfertilized soil having a soil solution concentration of $0.17 \mu\text{M}$. For bean the influx remained nil up to $0.53 \mu\text{M}$. Therefore, C_{imin} was assumed to be $0.1 \mu\text{M}$ for all species, except bean where it was $0.5 \mu\text{M}$. These values agree with data from solution culture (Jungk, 1974; Nielsen and Barber, 1978; Breeze *et al.*, 1984).

K_m : the Michaelis constant, (mol cm^{-3}), is the difference between the concentration at which influx is half I_{\max} and C_{imin} . The value for K_m was derived from flowing solution culture experiments of Asher and Longergan (1967) and Breeze *et al.* (1984). They have shown that plants which grow at constant low concentration reach almost maximum growth at P concentrations of 0.2 to $1.0 \mu\text{M}$. Therefore, for most species, a K_m value of $0.4 \mu\text{M}$ seems to be realistic. This value was checked by a procedure of Seeling and Claassen (1990) that determines kinetic parameters by model calculations. The procedure is based on measured P influx from soils of different soil solution concentrations. Furthermore, it is assumed that P is mainly taken up by root hairs. The calculations confirmed the K_m value of around $0.4 \mu\text{M}$, with exceptions for wheat and ryegrass which had K_m values of 2.3 and $1.3 \mu\text{M}$, respectively (see Table A2).

r_0 : root radius, cm. An average value for the whole root system was obtained from root length, RL (cm) and root fresh weight, W_R (g), by

$$r_0 = \sqrt{W_R / (\pi RL)} \quad (3)$$

Table 2. Phosphorus influx (I_n) of seven plant species in relation to morphological root properties (root radius, r_0 , and root hairs) and cation and anion uptake balance ($\Sigma A^- - \Sigma C^+$). (P application: 5 mg/100 g)

Species	I_n $\frac{10^{-14} \text{ mol}}{\text{cm s}}$	r_0 10^{-2} cm	Root hairs			$\Sigma^- - \Sigma C^{+a}$ $10^{-9} \text{ eq cm}^{-1}$	Ca uptake
			Number per mm	Av. length (mm)	SA ^b ($\text{cm}^2 \text{ cm}^{-2}$)		
Onion	0.84	2.29	1	0.05	6.5×10^{-3}	n.d.	198
Ryegrass	0.69	0.66	45	0.34	1.2	62	12
Wheat	0.91	0.77	46	0.33	1.2	110	21
Rape	3.20	0.73	44	0.31	1.3	227	141
Tomato	1.86	1.00	58	0.17	0.6	5	335
Spinach	4.85	1.07	71	0.62	1.9	19	93
Bean	0.60	1.45	49	0.20	0.4	87	269

^a $\Sigma C^+ = K^+ + Ca^{2+} + Na^+ + Mg^{2+}$

$\Sigma A^- = H_2PO_4^- + SO_4^{2-} + Cl^- + \text{total N (uptake of N assumed as } NO_3^-)$.

^b SA = surface area of root hairs in cm^2 per cm^2 root cylinder surface area.

r_1 : the mean half distance between roots (cm) was calculated from root length densities, L_v (cm cm^{-3} soil) by

$$r_1 = 1/\sqrt{(\pi RL_v)} \quad (4)$$

v_0 : water influx. An average value of $2.7 \times 10^{-7} \text{ cm}^3 \text{ cm}^{-2} \text{ s}^{-1}$ was assumed. The size of v_0

does not need to be determined with accuracy because mass flow is negligible for P solution concentrations of a few $\mu\text{mol L}^{-1}$ (see Table 2).

k : the relative root growth constant (s^{-1}) calculated by

$$k = (\ln RL_2 - \ln RL_1)/(t_2 - t_1) \quad (5)$$

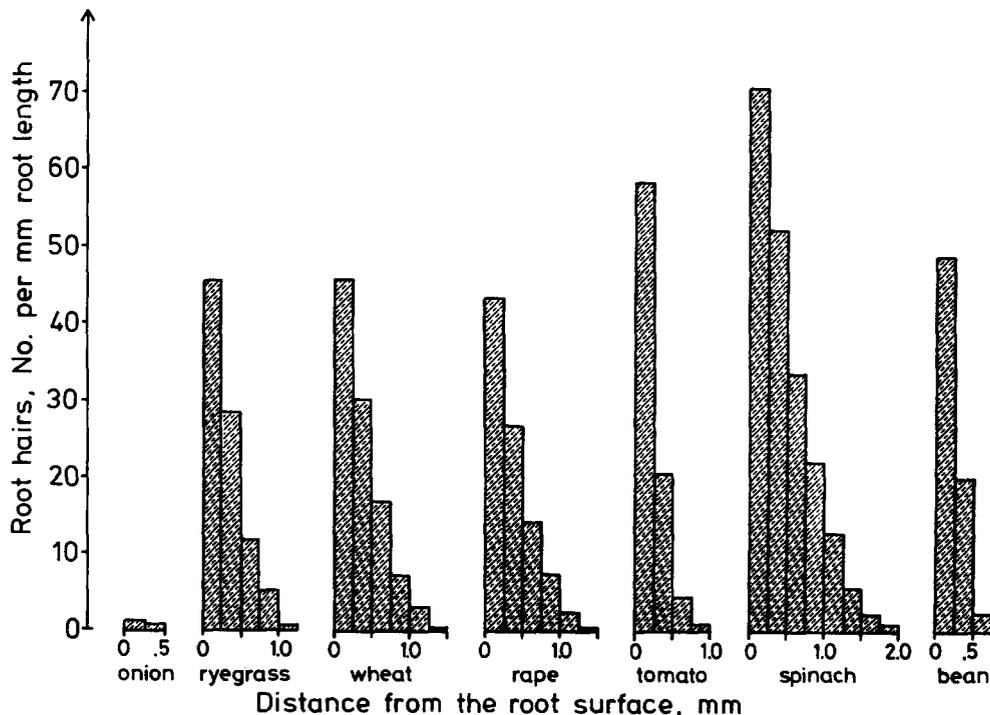


Fig. 1. Root hair distribution for seven plant species. The soil around roots was divided into cylindrical compartments of 0.25 mm walls. Each bar represents the number of root hairs that reach into or cross the respective compartment. Values are averaged over all P treatments.

For model calculations which include P uptake by root hairs, the radius, number and length distribution of root hairs must be known as well as their uptake parameters I_{\max} and K_m . The latter were assumed to be the same as for the root cylinder surface (see I_{\max}). Root hair radius, r_{0h} , was set at 5×10^{-4} cm, as reported by Drew and Nye (1969) and Barber (1984). Root hair distribution is shown in Figure 1. From these values, the mean half distance between root hairs, r_{1h} , in each compartment of 0.25 mm thickness was calculated by

$$r_{1h} = \sqrt{V/(\pi L_h)} \quad (6)$$

where V is the volume of the annular compartment around the root and L_h the total length of root hairs in this volume.

Both models calculate nutrient depletion around roots and uptake by 1 cm of root segment as a function of time. Using this function together with the root growth curve given by RL_1 and k (Table A3), the uptake, U , of the whole root system can be calculated (Claassen *et al.*, 1986). From total uptake, an average influx, I_n , ($\text{mol cm}^{-1} \text{s}^{-1}$) was calculated by the formula of Williams (1948)

$$I_n = U k / (RL_2 - RL_1) \quad (7)$$

where RL_2 , the root length at the second harvest, was obtained from RL_1 using the exponential root growth function

$$RL_2 = RL_1 \exp(k(t_2 - t_1)) \quad (8)$$

Results and discussion

Relationship between P influx and morphological and physiological properties of the root

Root hair properties are shown in detail in Figure 1 and summarized in Table 2. Root radius and cation-anion uptake balance are also shown in Table 2. Density and length of root hairs varied widely; spinach having the highest density (71 per mm), and greatest length (0.62 mm). These properties gave spinach a root hair surface

area twice that of the root cylinder alone, thereby increasing total root surface area by a factor of 3. Other species had less and shorter root hairs. Root radius, the other morphological property studied, varied from 0.66×10^{-2} cm for ryegrass to 2.29×10^{-2} cm for onion.

Cation-anion uptake balance was expressed in ion equivalents per cm root. In all cases, anion uptake was larger than cation uptake indicating an excretion of HCO_3^- into the rhizosphere. This excretion would increase the pH in the rhizosphere but at the same time decrease Ca activity in equilibrium with the CaCO_3 present in the soil. Using the solubility product of octocalciumphosphate, $\text{Ca}_4\text{H}(\text{PO}_4)_3 \times 2.5 \text{H}_2\text{O}$, (Thomas, 1974) and of CaCO_3 (Adams, 1974), Föhse (1985) deduced the following equation relating HPO_4^{2-} to the HCO_3^- and H^+ activity

$$(\text{HPO}_4^{2-})^3 = k \frac{(\text{HCO}_3^-)^4}{(\text{H}^+)^2} \quad (9)$$

where k is a lumped constant of several solubility constants. This equation shows that in a soil with free CaCO_3 , an increase in HCO_3^- concentration increases P solubility. In fact, this is the basis for the extraction procedure for P by NaHCO_3 after Olsen *et al.* (1954). Therefore, in our experiment, a larger uptake of anions than cations would increase P availability in the rhizosphere. This effect may be further enhanced by a decrease of the Ca concentration in the rhizosphere. Calcium uptake per cm of root is shown in the last column of Table 2. Cation-anion uptake balance varied from 5×10^{-9} eq cm^{-1} for tomato to 227×10^{-9} eq cm^{-1} for rape, with no clear differentiation between monocots and dicots. In contrast, Ca uptake was low for the gramineous species wheat and ryegrass (12 and 21×10^{-9} eq cm^{-1}), and high for the dicots up to 335×10^{-9} eq cm^{-1} for tomato.

The objective of this paper was to investigate whether the root properties described above can explain the differences in P influx shown in Table 2. The results indicate, that onion with the largest root radius had one of the smallest P influxes. Spinach with the highest influx of 4.85×10^{-14} mol $\text{cm}^{-1} \text{s}^{-1}$ had the highest root hair density and the longest root hairs. On the

contrary, ryegrass, wheat and rape had almost the same root radius and root hair density, but differed in P influx by a factor of 4 (from $0.69 \times 10^{-14} \text{ mol cm}^{-1} \text{ s}^{-1}$ to $3.20 \times 10^{-14} \text{ mol cm}^{-1} \text{ s}^{-1}$). Even though onion was devoid of root hairs, it had an influx similar to ryegrass or bean. Further inspection of the remaining factors, i.e. cation-anion balance and Ca uptake, show that there was no clear relationship between them and P influx. The average values of cation-anion balance used here may have masked the effect of a possibly locally enhanced acidification. Hoffland *et al.* (1989) observed that rape seedlings acidified the rhizosphere along a 1.5 cm root zone behind the root tip by exuding organic acids.

These results show clearly that no single factor alone can explain the differences in P influx among plant species. In order to separate the influence of these factors, model calculations were used.

Model calculations

Model calculations of P influx were done for roots with or without root hairs, except for onion which had no hairs. The parameters used for these calculations are listed in Tables A1, A2, A3 (see appendix) and Table 2. Figure 2 shows the comparison of calculated to measured P in-

flux of onion and spinach as a function of P concentration in soil solution.

For onion calculated influx was as high as or somewhat higher than the measured value when soil solution concentration was higher than $1 \mu\text{M}$ P. Hence, under these conditions P uptake by onion was realistically simulated by the model. However, at low P concentration, calculated influx was only 30% of the measured value. The reason for this discrepancy can be attributed to factors or processes not included in the model. Some of them were mentioned in the Introduction. Nevertheless, it may also be due to the fact that at low P concentration (P application: $2 \text{ mg}/100 \text{ g}$), the growth of onion was very small resulting in inaccurate measurement of P influx (see Figs. 1 and 3 of Föhse *et al.*, 1988).

For spinach calculations, neglecting root hairs gave influxes of only 10 to 40% of the measured data. However, when root hairs were included, calculated and measured influx was in close agreement. This shows that in spinach root hairs are necessary to explain the observed P influx. It also indicates that in soils of low P content root hairs may contribute as much 90% of total P uptake. This is consistent with Lewis and Quirk (1967), Hendriks *et al.* (1981) and Bhat *et al.* (1976) who explained the width of the P depletion zone around roots by the function of root hairs.

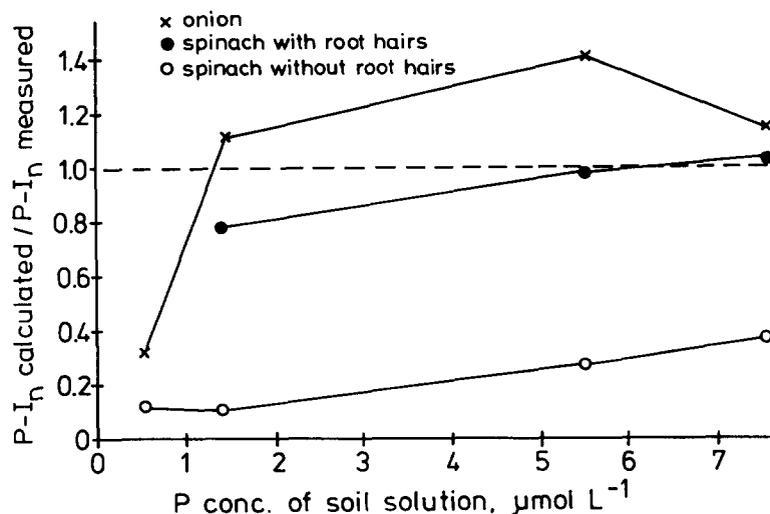


Fig. 2. Comparison of measured and calculated P influx of spinach and onion at different P levels in soil. Calculations were performed with simulation models that neglect root hairs (onion and spinach) or include root hairs (spinach).

A comparison of calculated and measured P influx for all species at several P levels in soil (see Table A3), including the values listed in Table 2, is presented in Figure 3. When root hairs were neglected in the calculation (Fig. 3a), only the calculated data for onion and bean are close to the 1:1 line. The other species are far below this line, as already discussed for spinach. When root hairs were included in the model (Fig. 3b), calculations show that most points are near the 1:1 line. Thus, in many plant species P uptake from soil largely depends on the contribution made by root hairs. This conclusion confirms results of Itoh and Barber (1983a, b) who also found that measured and simulated P uptake of several species only agreed, when allowance was made for P uptake by root hairs.

Even though the general agreement is close, some points, mainly those of tomato and rape, are still clearly below the 1:1 line. This would indicate that P influx is additionally influenced by factors or processes not included in the model. Table 2 shows that rape had a high excess of anion over cation uptake as well as a relatively high Ca uptake. Tomato had the highest Ca uptake of the species studied. As discussed before, both of these processes may enhance P availability, resulting in a calculated P influx being lower than the measured P influx.

Mode of action of root hairs

From Table 2, no close relationship between P influx and root hair density or length was found. Bole (1973) came to the same conclusion. This apparent contradiction to the results of model calculations may suggest a complex mode of action of root hairs other than to increase the absorbing root surface.

Calculated P concentration profiles around a spinach root (Fig. 4) show that the concentration at the root surface after 3 to 10 days is decreased to 10 or 15% of the initial value. This decrease is similar for roots with or without root hairs. However, the width of the P depletion zone differs greatly. For example, after 10 days of uptake at 80% of the initial soil solution concentration, P depletion extends to 0.23 mm without root hairs, but to 0.78 mm with root hairs. The difference in P uptake is even larger, *i.e.* proportional to the square of the radius of the depletion zone, because of the cylindrical geometry of the root. The small extension of the P depletion zone is due to the low effective diffusion coefficient of phosphorus ($3.7 \times 10^{-10} \text{ cm}^2 \text{ s}^{-1}$). Therefore, the P depletion profile of the root with root hairs is largely determined by root hair distribution. With spinach having the highest root hair density, there is no complete exhaus-

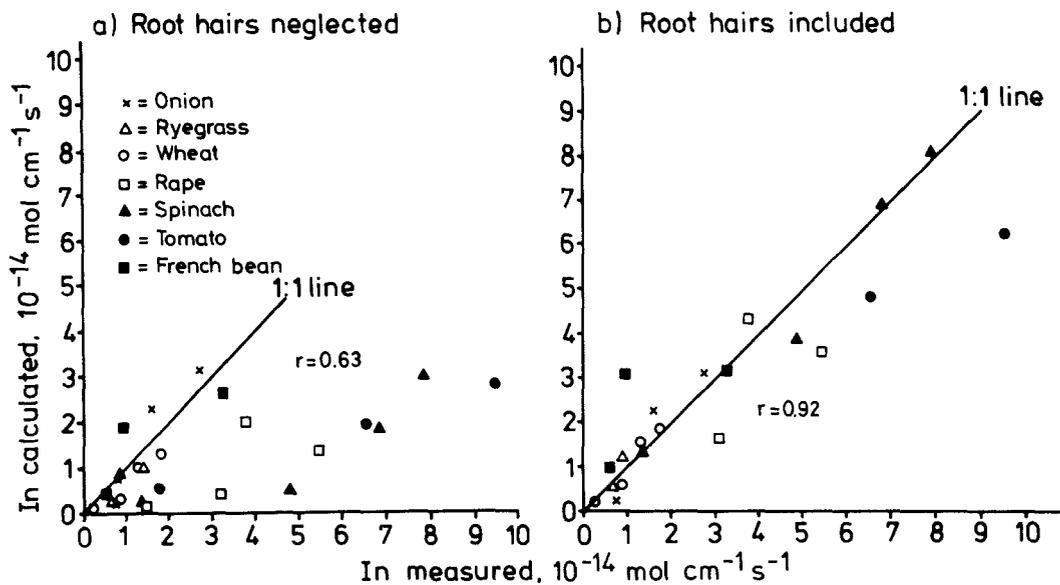


Fig. 3. Comparison of measured and with a simulation model calculated P influx (I_n) for seven plant species. a) root hairs neglected in the model, b) root hairs included in the model.

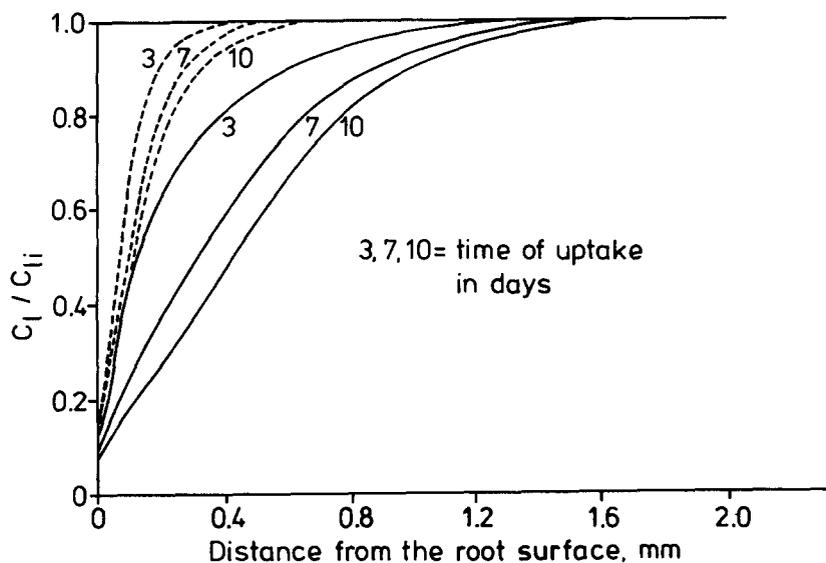


Fig. 4. Phosphorus concentration profiles around a root of spinach as calculated by a model for roots with (—) and without (---) root hairs. C_i/C_{ii} is the ratio of soil solution concentration (C_i) to the initial soil solution concentration (C_{ii}).

tion of P in the region of root hairs as was found by Hendriks *et al.* (1981) and other authors who applied autoradiographic procedures. With this technique, roots were grown along a glass plate leading to a root hair density higher than natural and by using ^{33}P , a soil layer of only 3 mm thickness was studied (Hendriks, 1980). Therefore, this procedure probably overestimated the significance of root hairs. Gahoonia (1987), using the soil thin-slicing technique of Kuchenbuch and Jungk (1982), did not find this exhaustion of P in the root hair zone.

Figure 5 shows the time course of calculated P uptake of 1 cm of root segment of spinach with root hairs, and of its root cylinder. For comparison the time course of P uptake of a root devoid of root hairs is also shown. The root with root hairs takes up as much P in one day as a root devoid of root hairs in 10 days. Phosphorus uptake continued almost linearly up to day 10. According to the model calculation, of the total of 28 nmol cm^{-1} , only 2.2 nmol cm^{-1} were taken up by the central root cylinder, but 92% by root hairs.

The importance of root hairs for P uptake in soils low in P is based on 3 features:

- increase of absorbing surface
- very low radius
- accessibility of a larger soil volume

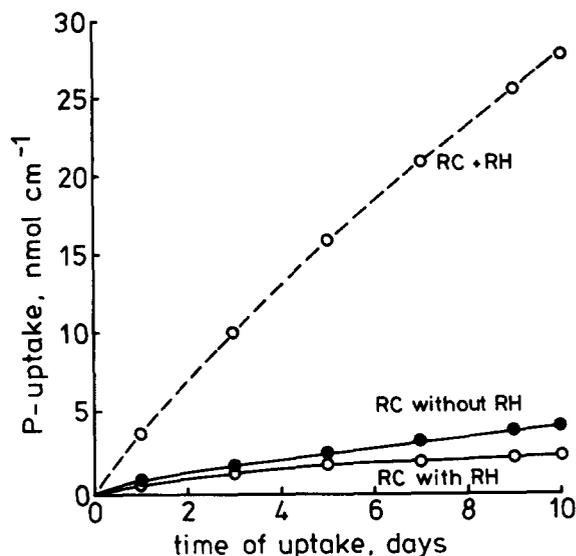


Fig. 5. Cumulative phosphorus uptake by one cm of spinach root as calculated by simulation models. RC + RH = uptake by roots with root hairs; RC without RH = uptake by root cylinders devoid of root hairs; RC with RH = uptake by root cylinders of roots having root hairs. (P application: 5 mg P/100 g).

Absorbing surface area

Table 2 shows that the surface area of root hairs varies among species. For bean it is about 40%, for wheat, ryegrass and rape about equal, and for spinach almost twice that of the root cylin-

der. An increased absorbing surface means a lower required influx per unit surface area. For plant species like spinach, root hairs increased the absorbing surface by 200%, although influx per cm of root increased by as much as 700% (see Fig. 2). The enlargement of the surface area is therefore not sufficient to explain the increased influx due to root hairs.

Root hair radius

Root hair radius is about 5×10^{-4} cm (Barber, 1984) *i.e.* 20–30 times smaller than the radius of the root cylinder. Because of the small radius a higher volume of soil and thereby a higher amount of nutrient is in close vicinity of each unit of absorbing surface. Therefore, P concentration at the root surface is lowered to a lesser degree and influx proceeds at a higher rate. This effect as well as the interaction of the radius of the absorbing surface with the uptake parameter I_{\max} is visualized for rape and wheat in Figure 6 and Table 3. Both species had similar quantities of root hairs, but very different P influx (Table

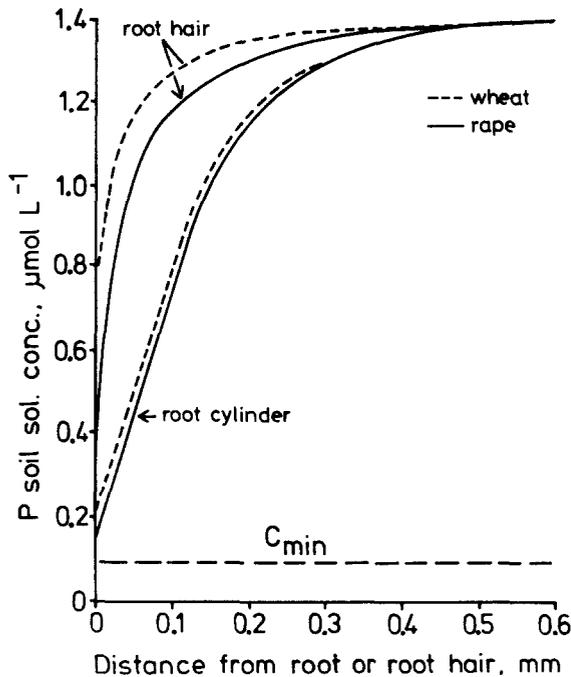


Fig. 6. Calculated concentration profiles of P around wheat and rape roots or root hairs. ($C_i = 1.4 \mu\text{mol L}^{-1}$; $b = 1500$; $D_e = 3.7 \times 10^{-10} \text{ cm}^2 \text{ s}^{-1}$; period of uptake: 6 days; P application: 5 mg P/100 g).

Table 3. Effect of I_{\max} (maximum influx) on calculated influx per cm^2 of root cylinder or root hair. (P application: 5 mg/100 g)

Species	I_{\max}	I_n	I_n
	root cylinder	root hair	
($10^{-14} \text{ mol cm}^{-2} \text{ s}^{-1}$)			
Wheat	33	7.8	20
Rape	98	8.3	34

r_0 – root cylinder = 0.01 cm.

r_0 – root hair = 0.0005 cm.

2) and I_{\max} values (Table A2). For both species, the P concentration at the root cylinder surface was lowered to a similar value (Fig. 6) close to the minimum concentration (C_{\min}). The concentration gradient was therefore similar for both species and so was the calculated influx (Table 3). In contrast, when P uptake proceeds by root hairs, the concentration decreased to about 50% of its initial value for wheat but to 25% for rape (Fig. 6). In spite of this smaller decrease, the concentration gradient was steeper because of the smaller extension of the depleted zone. The steeper gradient caused a larger flux by diffusion, and the higher concentration at the root hair surface caused a higher influx. Phosphate influx increased from 7.8×10^{-14} to $20 \times 10^{-14} \text{ mol cm}^{-2} \text{ s}^{-1}$ for wheat and from 8.3×10^{-14} to $34 \times 10^{-14} \text{ mol cm}^{-2} \text{ s}^{-1}$ for rape (Table 3).

Rape decreased the P concentration more than did wheat because of its larger I_{\max} value. Such a difference in concentration decrease was not obtained when P uptake was calculated from the root cylinder, because both species lowered the P concentration to almost the lowest value possible (Fig. 6). This shows that differences in uptake parameters, like I_{\max} , may become effective only when P uptake proceeds mainly through root hairs. This interaction between radius and I_{\max} is assumed to be the main reason for the lack of a close correlation between root hair length and P influx (Table 2).

Accessibility of a larger soil volume

As root hairs grow perpendicular to the root cylinder they drive nutrient absorbing surface into the soil. This increases the amount of nutrient accessible to a unit root length in two ways. Firstly, the nutrients within the root hair

Table 4. Phosphorus uptake, U, from inside and outside the root hair cylinder, as calculated by the simulation model. (P application: 5 mg/100 g)

Root hairs ^a	U, nmol P/cm in 18 days		
	Root hair cylinder		total
	inside	outside	
Without	–	4.8	4.8
With	6.5	7.2	13.7

^a All root hairs were regularly distributed around the root within a cylinder of 0.03 cm thickness.

cylinder are very close to the absorbing surface, and secondly, the quantities of nutrients flowing from the bulk of the soil towards the root surface are larger when root hairs are present. This latter effect is comparable to that of an increase in root radius, but is more effective. Table 4 describes these two effects for a rape root. The calculations show that P diffusion to a root without root hairs amounted to 4.8 nmol cm⁻¹ root length in 18 days. In comparison, 7.2 nmol cm⁻¹ root length entered the root hair cylinder from outside. Since 13.7 nmol cm⁻¹ was the total amount taken up, 6.5 nmol have come from within the root hair cylinder. For this calculation, root hairs were confined to an annular element of 0.03 cm. In nature, where root hairs have different lengths, the effect described also exists but cannot be quantified as in Table 4.

The significance of root hairs for the P nutrition of plants

If influx at high P concentration, expressed by I_{\max} , is regarded as a measure of the P demand of a plant required for maximum growth, the ratio of the actual influx (I_n) to I_{\max} is then a measure of the extent to which this demand is being satisfied. Figure 7 shows for the P addition of 5 mg/100 g that this ratio increased with increasing root hair surface. Thus, in a soil with low P availability, plants with abundant long root hairs can obtain a larger fraction of maximum yield than plants with few or no root hairs.

The relationship shown in Figure 7, which takes into account root hairs only, but not the root/shoot ratio, is mainly a consequence of the small radius of root hairs. Consequently the

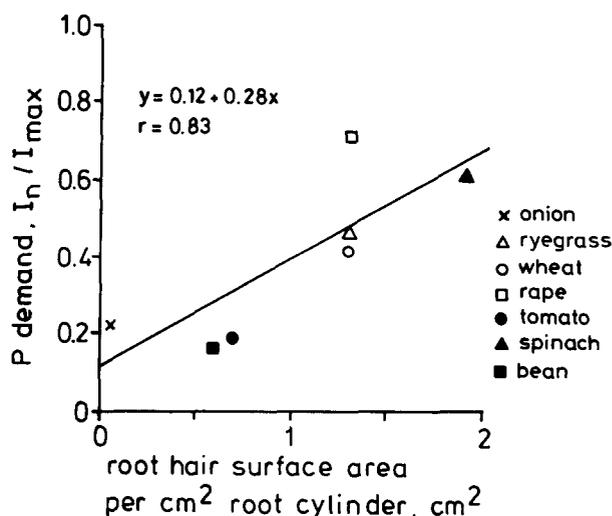


Fig. 7. The significance of root hairs for satisfying the P demand of the roots of seven plant species. (P application: 5 mg P/100 g).

concentration at the absorbing surface remained relatively high (Fig. 6) and the influx was then strongly determined by I_{\max} .

The results confirm that root hairs are a major factor in P acquisition by plants. They should therefore be included in breeding programs aiming at P-efficient plants.

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Appendix

Table A1. Estimation of the maximum P influx, I_{\max} , of spinach as a function of shoot P concentration. RC is the flux per unit root cylinder surface area and RC + RH per root cylinder plus root hair surface area

P application (mg/100 g)	Shoot P conc. (mg g ⁻¹)	$I_{\max} 10^{-14} \text{ mol s}^{-1}$		
		cm ⁻¹	cm ⁻² (RC)	cm ⁻² (RC + RH)
2	3.5	16.0	238	82.1
5	6.5	11.4	170	58.5
10	8.5	8.0	119	41.0
20	8.5	8.0	119	41.0
40	9.1	8.0	119	41.0
80	8.9	8.0	119	41.0

Table A2. Plant and soil properties used in the model calculations of P uptake

Plant species	$I_{\max}^a, 10^{-14} \text{ mol cm}^{-2} \text{ s}^{-1}$		K_m $\mu\text{mol L}^{-1}$	C_{min}
	(RC) ^b	(RC + RH) ^b		
Onion	26.8	–	0.4	0.1
Ryegrass	35.4	15.4	1.3	0.1
Wheat	50.8	22.1	2.3	0.1
Rape	97.9	42.6	0.4	0.1
Tomato	153.0	90.0	0.4	0.1
Spinach	119.0	41.0	0.4	0.1
Bean	38.7	27.6	0.4	0.1

Soil properties

P application mg/100 g	C_{ii} $\mu\text{mol L}^{-1}$	D_e $10^{-10} \text{ cm}^2 \text{ s}^{-1}$	b
2	0.53	3.52	1580
5	1.40	3.72	1500
10	5.50	7.29	762
20	7.55	5.00	1110
40	10.90	3.61	1540
80	10.40	1.72	3225

^a I_{\max} for the treatments of high P application only.

^b RC = root cylinder, RH = root hair

Table A3. Root length at first harvest, L_1 , cm per plant, root growth constant, k in 10^{-6} s^{-1} , and uptake time, $t_2 - t_1$, used for model calculations

Plant species	P application (mg per 100 g soil)								$(t_2 - t_1)$ days
	2		5		10		20		
	L_1	k	L_1	k	L_1	k	L_1	k	
Onion	76	0.44	102	0.56	130	0.79	85	1.12	14
Ryegrass			278	1.52	298	1.51	328	1.54	16
Wheat	452	1.48	374	1.72	512	1.53	488	1.52	18
Rape	478	1.45	487	1.78	216	2.02	409	1.88	15
Tomato			426	2.21	424	2.55	514	1.90	8
Spinach	668	1.53	607	1.62	380	2.11	550	2.51	10
Bean			1946	0.54	3046	0.89	1598	1.53	10