

Availability in Soil and Acquisition by Plants as the Basis for Phosphorus and Potassium supply to Plants

Albrecht Jungk and Norbert Claassen

Institut für Agrikulturchemie der Georg-August-Universität, Von-Siebold-Strasse 6, D-3400 Göttingen

Eingegangen: 19. Oktober 1988

Angenommen: 23. Januar 1989

Summary - Zusammenfassung

This report summarizes research aimed at describing the processes and quantifying the factors affecting transfer of P and K from soil into plants. Soil properties related to availability and plant properties reflecting nutrient acquisition were determined. Their interactions in the rhizosphere and their importance for nutrient supply of plants were studied by a combination of measurements and calculations using a simulation model.

Phosphorus and potassium uptake by roots decreased P and K concentration at the root surface and caused characteristic depletion profiles in the adjacent soil. The shape of the profiles depended on the effective diffusion coefficient, the concentration of the nutrient in soil, morphological properties of the roots and on influx into roots. The degree of depletion at the root surface indicated the proportion of the nutrient potentially available in the soil. The shape of the depletion profiles reflected the amount of the nutrient taken up by a root section. The parameters found to describe nutrient acquisition are (i) influx per unit root length, (ii) root length per unit shoot weight (root/shoot ratio), and (iii) the period of time a root section absorbs nutrients. Plant species differed considerably in these properties.

In order to integrate the processes involved and to evaluate the importance of individual factors, the Claassen-Barber model was used. Depletion profiles and nutrient uptake calculated with this model were in good agreement with measured values in a number of cases. However, at low P supply, plants absorbed substantially more P than the model predicted. This indicates that influx in this case is supported by mechanisms not properly taken into account yet.

Influx per unit root length depends on morphological properties of and nutrient mobilization by roots. Root hairs increase root surface area per unit root length. In addition, because of their small diameter and geometric arrangement in soil, root hairs are specially apt to gain from diffusion when concentration gradients are small. This applies even more to VA-mycorrhizae. Their hyphae are longer and thinner than root hairs and can thus deplete larger volumes of soil per unit root length.

Root-induced changes of soil pH increased the size of P depletion profiles, indicating that roots can mobilize soil P by this mechanism. Both acid and alkaline phosphatase enzyme activities were found to be markedly increased at the soil-root interface suggesting that soil organic P may contribute to the P supply of plants.

Verfügbarkeit im Boden und Aneignungsvermögen der Pflanzen als Grundlage für die P- und K-Versorgung von Pflanzen

Es wird zusammenfassend über Untersuchungen berichtet, die das Ziel haben, die Prozesse zu beschreiben und ihre Einflußgrößen zu quantifizieren, die den Übergang von P und K aus dem Boden in die Pflanze bestimmen. Hierzu wurden Bodeneigenschaften gemessen, die die Verfügbarkeit, und Pflanzeigenschaften, die das Aneignungsvermögen kennzeichnen. Ihre Wechselwirkungen in der Rhizosphäre und ihre Bedeutung für die Nährstoffversorgung von Pflanzen wurden durch eine Kombination von Messungen und Modellrechnungen untersucht.

Die P- und K-Aufnahme der Wurzeln führt zu charakteristischen Verarmungsprofilen im wurzelnahen Boden. Die Gestalt der Profile hängt vom effektiven Diffusionskoeffizienten und der Konzentration des Nährstoffs im Boden sowie vom Influx und von morphologischen Eigenschaften der Wurzeln ab. Die Konzentrationsabsenkung an der Wurzel ist ein Maß für den Anteil des Nährstoffs, der potentiell verfügbar ist. Die Form der Verarmungsprofile bezeichnet die Menge des Nährstoffs, die ein Wurzelabschnitt aufnimmt.

Das Aneignungsvermögen wurde durch (i) die Aufnahme rate (Influx) pro Einheit Wurzellänge, (ii) die Wurzellänge pro Gewichtseinheit Sproß (Wurzel/Sproß-Verhältnis) und (iii) die Dauer der Aufnahmeaktivität der Einzelwurzel gekennzeichnet. Pflanzenarten weisen große Unterschiede in diesen Merkmalen auf. Um festzustellen, inwieweit die Aufnahme der Pflanzen aus den beteiligten Prozessen berechenbar ist und um die Bedeutung der beeinflussenden Faktoren zu werten, wurde das Rechenmodell von Claassen und Barber angewendet. Es führte in einer Reihe von Fällen zu guter Übereinstimmung mit Messungen sowohl von Verarmungsprofilen im Boden als auch der Nährstoffaufnahme von Pflanzen. Bei geringer P-Versorgung haben die Pflanzen jedoch deutlich mehr P aufgenommen, als das Modell angibt. Daraus wird deutlich, daß der Influx unter diesen Bedingungen durch Mechanismen gesteigert wird, die das Modell bisher nicht angemessen berücksichtigt.

Der Influx pro Einheit Wurzellänge ist von der Gestalt der Wurzeln und von Mobilisierungsprozessen abhängig. Wurzelhaare tragen erheblich zur Wurzeloberfläche bei. Darüberhinaus zeigte sich, daß Wurzelhaare infolge ihres geringen Durchmessers und ihrer geometrischen Anordnung im Boden bei niedrigen Konzentrationen besonders effizient sind. Das gilt noch mehr für die Hyphen von VA-Mykorrhiza. Sie sind länger und dünner als Wurzelhaare und schöpfen pro Einheit Wurzellänge größere Bodenvolumina aus.

Wurzelinduzierte pH-Änderungen in der Rhizosphäre führten durch P-Mobilisierung zur Vergrößerung der P-Verarmungszone. Die Aktivität von Phosphatasen war in Wurzelnähe erheblich höher als im übrigen Boden. Dies deutet darauf hin, daß organische P-Verbindungen des Bodens für die P-Versorgung von Pflanzen von Bedeutung sein können.

Introduction

Nutrient supply to plants is the result of interactions between plant roots and soil. Research summarized by Nye and Tinker (1977) and Barber (1984) has revealed that nutrient supply to a plant depends generally on the quantity of the nutrient present and its mobility in soil ("availability") as well as on size, uptake kinetics and mobilizing capacity of the root system ("acquisition").

When plants absorb a nutrient, soil solution concentration decreases at the root surface, provided transport from soil toward the root is small. The equilibrium in soil is thus disturbed and a gradient created. The adjacent soil reacts in two ways:

- release of the nutrient from the solid soil phase into solution, and/or
- transport from the bulk of the soil to the root.

Nutrient uptake of a plant is determined by the influx per unit root, which in turn depends on the flux towards the root largely caused by concentration gradients, and the size of the root system. In order to make quantitative assessments of the supply to a particular plant on a particular site, it is necessary to integrate into a comprehensive concept the processes involved in the transfer from soil into plants and the factors affecting them. The mathematical model suggested by Claassen and Barber (1976) is an example of such a unifying concept. It provides the possibility to prove or disprove our perception of the system by simulating nutrient uptake. It can also be used to evaluate such steps in the total sequence which cannot be measured. However, before conclusions from such calculations can be drawn, the model must be validated.

The purpose of this report is to summarize results of our research aimed at a better understanding of the processes and quantification of the factors involved in the transfer of nutrients from soils into plants.

Materials and methods

The results and conclusions are based on a combination of the following methods and procedures:

- a) Long term field experiments

Material from several long term P and K fertilizer trials on Luvisols from loess in Lower Saxony with a crop rotation of sugar beet, winter wheat and winter barley, as described by Müller (1988).

- b) Pot experiments with various soils and plant species as described in the publications cited for the respective results.

- c) Measurement of nutrient depletion profiles at the soil-root interface by: (i) Quantitative autoradiography as described by Claassen et al. (1981 a), to measure nutrient distribution around single roots. (ii) Thin slicing of rhizosphere soil (Kuchenbuch and Jungk, 1982). In the latter technique root systems of a set of growing rape or ryegrass seedlings are separated from soil by a Nylon screen which allows root hairs and mycorrhizal hyphae but not roots to penetrate into the soil. This constitutes a planar system where nutrients, in contrast to single roots, move in one direction only. After harvest the soil is sliced into 0.1 mm layers. The samples, which have a defined distance from the layer of roots, are then analyzed by usual

methods. Soil solution concentration around roots was calculated from these data by means of desorption curves (Claassen et al., 1981 b).

- d) Simulation calculation, mainly based on the Claassen-Barber model modified as described by Claassen et al. (1986). To calculate the gradients required for a given influx, the equation published by Barraclough (1986) was used.

Results and discussion

Pattern of soil depletion

To understand the phenomenon of nutrient availability in soils in a quantitative sense, information is required on the change of the nutrient content in soil caused by nutrient uptake of plants. As an example, the distribution of Rb-86 (as a tracer for K) around a single maize root section is shown in Fig. 1. Within 3 days the soil solution concentration was decreased from 28 μM in the bulk soil to 1 μM at the root surface. This decrease severely disturbed the Rb equilibrium in soil. The depletion profile of total Rb shows that both, desorption of Rb from the solid phase and transport from the bulk soil toward the root must have occurred.

These profiles develop with time. Their shape depends on the balance between influx and replenishment (Claassen et al., 1981 b). Because of ion competition, K depletion at the root surface may influence Mg uptake. Since the K influx is higher, K will usually be depleted faster than Mg. An initial repression of Mg influx by K can thus be alleviated with time as found by Seggewiss and Jungk (1988).

The distance of diffusion and therefore the final shape of the profiles depends strongly on the effective diffusion coefficient, D_e (Jost, 1952; Jungk et al., 1982). Because D_e is affected by buffer power and water content of the soil (Nye, 1966), K depletion profiles vary with clay and water content as well as with K saturation of the soil (Claassen et al., 1981 b; Kuchenbuch et al., 1986).

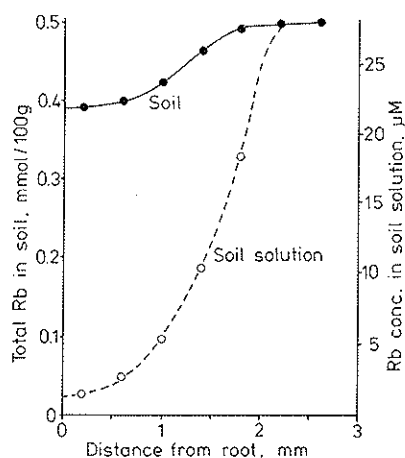


Figure 1: Depletion profile of Rb (^{86}Rb) in the soil and the soil solution adjacent to a maize root segment 3 days old. Bülten Luvisol from loess.

Abbildung 1: Rb-Verarmungsprofil des Bodens und der Bodenlösung in der Umgebung eines 3 Tage alten Maiswurzelabschnitts. Bülten Parabraun-erde aus Löss. (Claassen et al., 1981 b)

The degree of soil depletion has important effects on the rate and the amount of K released from the solid soil phase into solution. Desorption studies with a Luvisol from loess (Claassen and Jungk, 1982) have shown a strong release of the K fraction which is non-exchangeable with NH_4 , when the ambient solution decreased to 2 - 3 μM K. It is known that plants can deplete solutions well below this level. In agreement with this, at the root surface depletion of the HCl extractable K fraction of the soil was much stronger than was depletion of exchangeable K (Jungk et al., 1982; Kuchenbuch, 1983). It is therefore concluded that plants can mobilize large quantities of soil K by K depletion of the soil solution.

Previous fertilizer or cropping treatments may also be reflected by depletion profiles. The example for phosphate shown in Fig. 2 was obtained from a long term field experiment using the thin slicing technique (Kaselowsky, 1985). The initial HCl-soluble P content was 445 mg P/kg soil. In six years under a crop rotation of sugar beet, winter wheat, and winter barley the value decreased without P fertilizer application to 385 mg P/kg but increased to 485 mg P/kg with annual application of 80 kg P/ha. Bulk soil P content therefore changed slowly. In contrast, P content at the soil-root interface was decreased to 250 mg P/kg within a few days.

Assuming the total plough layer (4000 t soil/ha) would be depleted in P to the degree observed in Fig. 2 at the root surface, this quantity of P would be 940 kg/ha in the treatment

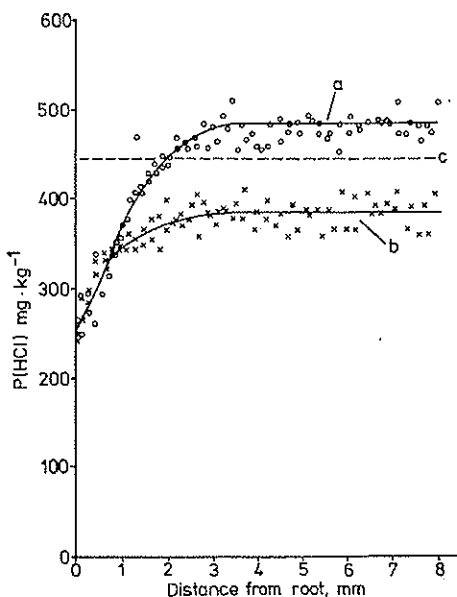


Figure 2: Effect of P application on P depletion profiles in the rhizosphere of rape root systems. Soil samples from a field experiment on Börry Luvisol from loess. a) Six years 80 kg P/ha annually, b) Six years without P fertilizer, c) Initial soil P content

Abbildung 2: Wirkung der P-Düngung auf P-Verarmungsprofile in der Rhizosphäre von Rapswurzelsystemen. Bodenproben aus einem Feldversuch in Börry auf Löss-Parabraunerde. a) Sechs Jahre 80 kg P/ha jährlich, b) Sechs Jahre ohne P-Düngung, c) P-Gehalt des Bodens zu Beginn des Versuchs. (Kaselowsky, 1985)

with P and 540 kg/ha without P application. The difference of 400 kg between these two treatments developed during the six years experimental period. This quantity is equivalent to 67 kg P/ha and year, a value which is fairly in agreement with the real balance between P fertilizer addition and P removal by plants. The degree of soil depletion at the root surface determined with this technique can be assumed to be almost the maximum possible, because of the planar experimental conditions. This depletion thus appears to be a parameter of the P fraction in soil which may be named potentially available. The word "potentially" emphasizes that this fraction, because of its chemical nature, can be utilized by the plants. In contrast, the fraction below 250 mg P/kg in Fig. 2 is unavailable in this sense. "Potentially", however, says nothing about the spatial availability and the rate of transfer from soil into plants which is the most important determinant of the supply to plants.

Nutrient requirements of plants

The depletion observed at the root surface has revealed that plants are able to create almost the maximum possible P and K concentration gradient between bulk soil and the root surface. This is important for the movement of nutrients toward the root surface because gradients are the driving force of diffusive flux. On the other hand, depletion may imply severe restrictions of influx into plants because influx depends on the concentration at the root surface.

Genus, species, and even varieties of the same species may differ in their ability to grow in soils of low nutrient content. This may be related to internal or external requirements (Föhse et al., 1988). The data in Table 1 were derived from a pot experiment with seven P levels. Both, P concentration in the plant and in the soil or the soil solution necessary to achieve 80% of maximum growth differed widely among species. Also, no correlation was found between internal and external P requirements. Wheat, for example, required 1.2 μM P in soil solution or 4 mg fertilizer P per 100 g soil and achieved 80% of maximum yield with 0.28% P in the dry matter. In contrast, the corresponding figures for onion were 6.9 μM P in soil solution, 17 mg fer-

Table 1: Internal and external phosphorus requirements of seven plant species for 80% of maximum growth (Holtensen Loess Subsoil)

Tabelle 1: Interner und externer Phosphor-Bedarf von sieben Pflanzenarten, um 80% des maximalen Wachses zu erreichen. (Föhse et al., 1988) (Löss-Unterboden Holtensen)

Plant species	P conc. % in d.m.	Soil soln. conc. μM P	Fertilizer application mg P/100 g soil
Onion	0.14	6.9	17
French bean	0.20	4.6	9
W.Wheat	0.28	1.2	4
Ryegrass	0.33	1.4	5
Rape	0.39	1.4	5
Tomato	0.45	5.7	11
Spinach	0.83	4.6	9

tilizer P, and 0.14% P in the dry matter. Because the plants grew in the same soil and environment it must be concluded that the differences were caused by differences in uptake efficiency of the root systems.

Root/shoot ratio (in terms of root length per unit of shoot weight), influx per unit root length, and the period of time a root section absorbs nutrients have been shown to be the factors determining nutrient supply of plants (Claassen and Jungk, 1984). The former two parameters were very different for the plants listed in Table 1. As shown in Fig. 3, wheat and ryegrass had high root/shoot ratios whereas spinach, rape and tomato were superior in P influx per unit root length when grown with limited P supply. The low shoot weight of onion and french bean in Fig. 3 can be attributed to their low uptake efficiencies because both root/shoot ratio and influx were low. The higher uptake efficiencies of the other species were mainly due to either a high root/shoot ratio or high influx. The differences in influx could not be explained on the assumption that P had moved from soil towards roots of cylindrical shape because P transport from soil was the rate limiting step (see Fig. 6 "root cylinder").

What are the reasons for these differences? This question can be answered only if the whole complex affecting nutrient supply is taken into account. The model of Claassen and Barber (1976) integrates the soil and plant factors affecting nutrient transfer from soil into the plant. It is based on the mechanisms of transport from soil toward roots by mass flow and diffusion, and uptake kinetics of roots. It makes allowance also for the size and growth rate of the root system. Barber (1984) found good agreement between calculated and measured P and K uptake values. Claassen et al. (1986) obtained very similar values for measured and calculated K depletion profiles of rape seedlings in soil. The model can therefore be regarded as giving a realistic picture of the soil-root system in terms of nutrient uptake.

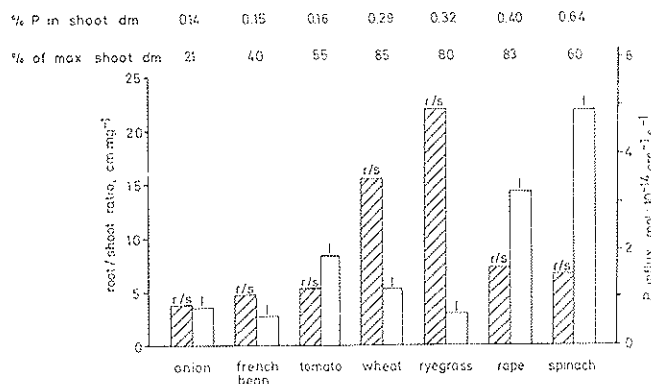


Figure 3: Phosphorus concentration, relative growth, root/shoot ratio and P influx of seven plant species grown in a low P loess subsoil treated with 5 mg P/100 g soil. Maximal growth was obtained with 40 mg P/100 g soil
Abbildung 3: Phosphor-Gehalt, Relativvertrag, Wurzel/Sproß-Verhältnis und P-Influx von sieben Pflanzenarten. Ein P-armer Löss-Unterboden wurde mit 5 mg P/100 g Boden gedüngt. Das maximale Wachstum wurde mit 40 mg P/100 Boden erzielt. (Föhse et al., 1988)

Using this model (Claassen et al., 1986), Müller (1988) studied P uptake of field crops on long term field experiments. The results shown for winter wheat in Fig. 4 are derived from plots under a sugar beet - grain crop rotation which had been treated annually without P or high quantities of fertilizer P for 20 years. As shown in Fig. 4, calculated and measured P uptake of wheat were in reasonably close agreement in case of the high P application. However, without fertilizer P, wheat took up substantially more phosphorus than the model predicted. Influx of P was thus underestimated in this case.

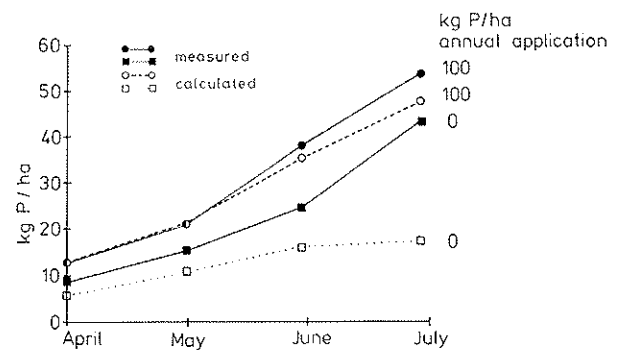


Figure 4: Phosphorus uptake of winter wheat measured in a field experiment and calculated by the Claassen-Barber model resp.
Abbildung 4: Phosphor-Aufnahme von Winterweizen im Feldversuch gemessen und mit dem Claassen-Barber-Modell berechnet (Versuch Höckelheim, Müller, 1988)

Factors affecting influx

Root morphology.

Root hairs have been shown to influence nutrient uptake efficiency of roots (Lewis and Quirk, 1967; Bhat and Nye, 1973, 1974; Föhse, 1985). Another root property affecting the contact between soil nutrients and the root surface is root radius (Barber, 1984; de Willigen and van Noordwijk, 1987). As shown in Table 2, marked differences between species were observed in root radius and both number and surface area of root hairs per unit root cylinder. With the exception of onion, root hairs contribute considerably to the total root surface area. Föhse and Jungk (1983) observed in nutrient solution culture that root hair formation was inversely related to P supply, a mechanism, which can thus be regarded significant in regulating uptake efficiency of the plants.

The Claassen-Barber model was used to quantify the influence of root hairs. The original model, which did not include root hairs, resulted in the data shown in Fig. 5a. Except for the low range, in most cases calculated influx was lower than measured influx. Acceptable agreement was obtained only with onion and french bean, the species which had the smallest proportion of root hairs (Table 2). If, however, root hairs were included by a calculation procedure developed by Claassen and Syring (in preparation), agreement with measured values was much better, (Fig. 5b).

Table 2: Morphological properties of roots of seven plant species (calculated from data of Föhse, 1985)

Tabelle 2: Morphologische Wurzeigenschaften von sieben Pflanzenarten

Plant species	Root radius mm	Root Hairs			
		density	average length	total length	surface area
		number mm r l	mm r h	mm r h mm r l	mm ² r h mm ² r a
Onion	0.229	1	0.05	0.3	0.1
French bean	0.145	49	0.20	11.8	0.4
W. wheat	0.077	46	0.33	20.4	1.3
Ryegrass	0.066	45	0.34	17.1	1.3
Rape	0.073	44	0.31	18.6	1.3
Tomato	0.100	58	0.17	13.7	0.7
Spinach	0.107	71	0.62	41.4	1.9

radius of root hairs = 0.005 mm

r h = root hair

r l = root length

r a = root axis

It can therefore be concluded that P influx per unit root length was strongly enhanced by root hairs. This can be explained by the enlargement of the root surface and because root hairs penetrate the soil perpendicular to the root axis. This gives access to a larger volume of soil per unit root length. Consequently, P depletion profiles were found to differ in their radial extension depending on root hair length (Hendriks et al., 1981).

If P or K availability in soil limits influx into the plant, diffusive flux from soil to root must be regarded as the limiting process. Diffusive flux depends on the size of the concentration gradient, provided other chemical soil properties remain unchanged. Gradients around roots may be defined as the difference in soil solution concentration between bulk soil and root surface. If the initial P and K concentration is low, gradients cannot be high. In this situation, a root system will be superior which can collect nutrients efficiently with smaller gradients than another.

What is the relation between root hairs and these gradients? In field experiments Claassen and Jungk (1987) found P and K influxes in field crops as shown in Table 3. Diffusive fluxes from soil to roots must equal influx. The concentration gradients necessary for such fluxes were calculated

Table 3: Measured P and K influxes, I_n , and calculated gradients in soil solution concentrations, ΔC_i , required for these fluxes

Tabelle 3: Gemessene P- und K-Influxe, I_n , und berechnete Konzentrationsgradienten in der Bodenlösung, ΔC_i , die der entsprechende Diffusionsfluß erfordert

Crop	I_n		ΔC_i	
	P mol · 10 ⁻¹⁴	K cm ⁻¹ s ⁻¹	P μM	K
Winter wheat	0.9	9	6	27
Winter barley	1.6	10	11	31
Sugar beet	2.5	25	19	86
Winter wheat Root hairs*	0.045		0.4	

* 20 cm total root hair length per cm root, diameter 5 μm

culated by means of the equation published by Barraclough (1986). If influx proceeded through the surface of the root cylinder only (root hairs neglected), these gradients had to range from 6 - 19 μM P and 26 - 86 μM K as shown in Table 3. However, such high gradients cannot be created because the initial concentration in soil solution is often lower. Yields were in fact unrestricted by P and K.

As shown in Table 2, wheat had a total root hair length of 20 cm per cm of root. If uptake is assumed to proceed through root hairs only, influx per cm root hair would be 0.045 · 10⁻¹⁴ mol · cm⁻¹s⁻¹ (Table 3). The P concentration gradient necessary to meet this influx would be as low as 0.4 μM P soil solution, less than a tenth of that when hairs were neglected.

This necessary gradient may in reality be not quite as low because competition between root hairs was not taken into account. The result, however, demonstrates the order of magnitude. The result implies that root hairs are more efficient in absorbing phosphate than root cylinders when influxes per unit area are compared. This conclusion follows from the fact that the root hairs of wheat had a surface area of 1.3 times that of the root cylinder they emerged from whereas the gradient necessary to drive diffusion was less than a tenth.

The effect of root hairs can be further elucidated by comparing depletion profiles of roots and root hairs. As shown in Fig. 6, which was calculated with the Claassen-Barber

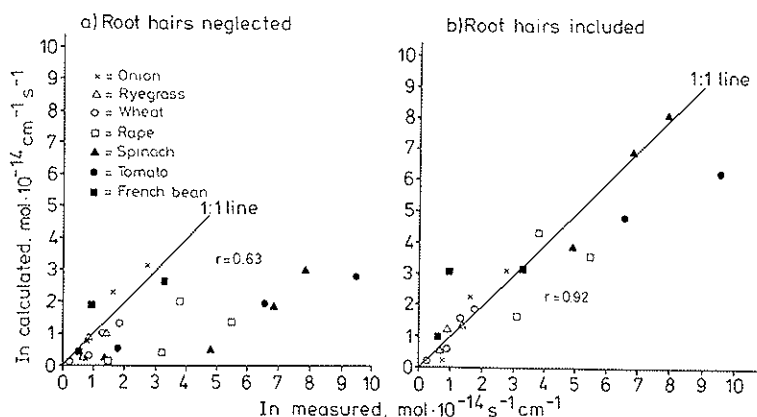


Figure 5: Phosphorus influx per unit root length of seven plant species. Comparison of measured and calculated influx without (a) and with (b) consideration of root hairs

Abbildung 5: Phosphorinflux von sieben Pflanzenarten pro Einheit Wurzellänge. Vergleich von gemessenem und berechnetem Influx ohne (a) und mit (b) Berücksichtigung der Wurzelhaare

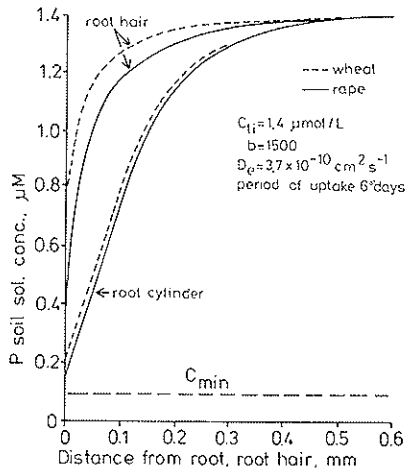


Figure 6: Calculated P depletion profiles of wheat and rape roots or root hairs using parameters of a loess-derived soil low in available P
Abbildung 6: Berechnete P-Verarmungsprofile der Wurzeln und der Wurzelhaare von Weizen und Raps unter Verwendung der Parameter eines P-armen Lössbodens

model, a root cylinder devoid of hairs creates a depletion profile larger in both, degree of depletion and width of the depleted zone than does an individual root hair. Phosphorus concentration at the root hair surface will therefore remain at a higher level than at the surface of the root cylinder. Uptake kinetics assumed to be equal, root hairs can thus maintain higher influx. The major benefit of root hairs in P supply of plants therefore seems to be that they enable the root system to operate effectively with low concentrations in the soil solution. This demonstrates the importance of diameter and the peculiar geometric arrangement of root hairs in soil.

Mobilization of nutrients by root exudates.

A change in the chemical environment of roots by substances released from roots is another strategy of plants to acquire nutrients of low solubility. Its importance for P and K supply is not well understood. It is known that plants can change the pH of the rhizosphere, which may influence the solubility of phosphate (Hedley et al., 1982; Bekele et al., 1983). To assess the influence of root-induced pH change on P availability, Gahoonia (1987) applied different sources of N. In a Luvisol containing P mainly as Ca phosphates, P depletion profiles were enlarged by NH₄- compared to NO₃-N as shown in Fig. 7. In contrast, with an Oxisol it was NO₃-N which caused a similar enlargement of the P depletion profile.

In soils close to or above pH 7, NO₃ is usually the main source of N. This tends to increase soil pH. In such soils Ca phosphates prevail, and their solubility is decreased with increasing pH. Therefore, a root-induced pH increase is not likely to mobilize P in such a soil. However, with rape seedlings, acidification was found even with NO₃ nutrition (Hedley et al., 1982). In Oxisols on the other hand, NO₃ nutrition, which causes pH increase, would be advantageous.

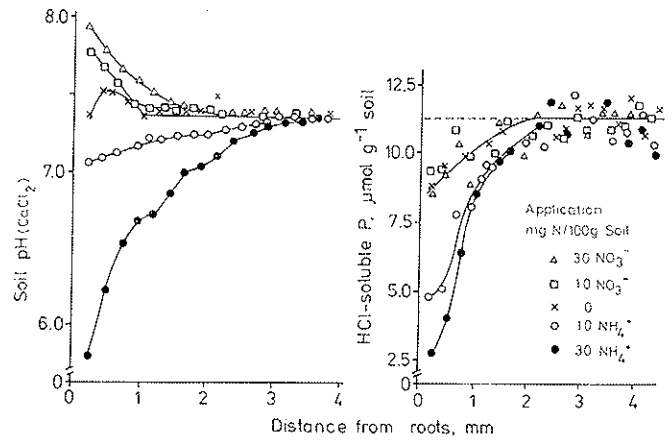


Figure 7: pH change and P depletion in soil caused by ryegrass in 10 days as affected by ammonium and nitrate nitrogen nutrition. Söderhof Luvisol from loess
Abbildung 7: Einfluß von Ammonium- und Nitrat-N-Ernährung auf pH-Änderung und P-Verarmung des Bodens durch Weidelgras in 10 Tagen. Söderhof-Parabraunerde aus Löss (Gahoonia, 1987)

Mobilization may also occur in the organic P fraction. It is known that phosphatase enzyme activity is higher at the soil-root interface than in bulk soil (Tarafdar and Jungk, 1987). In a sterile system Tarafdar and Claassen (1988) found that roots of clover hydrolyzed phosphate from phytate, glycerophosphate and lecithin at rates even higher than P influx into plants. This demonstrated that roots and not only rhizosphere microorganisms can hydrolyze organic P compounds. The conclusion can therefore be drawn that organic soil P mobilized by root-released enzymes, may also play a role in P nutrition of plants.

Mycorrhizae.

Mycorrhizal symbioses are known to improve P supply of plants in soils low in P. The mechanisms of this effect have

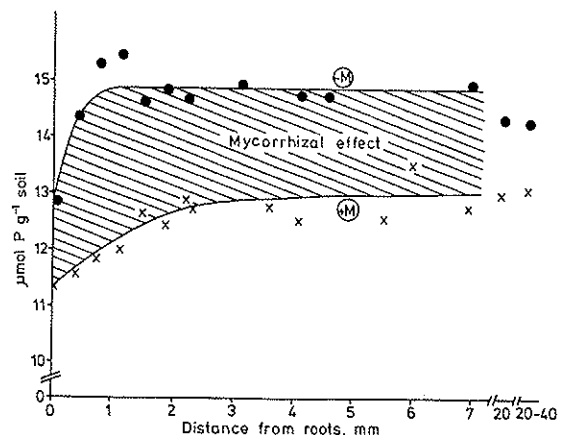


Figure 8: Effect of VA mycorrhiza on the P depletion of an Oxisol pH (CaCl₂) 5.3 caused by Capsicum annuum. Duration of experiment 14 weeks
Abbildung 8: Einfluß von VA-Mykorrhiza auf die P-Verarmung eines Oxisols pH (CaCl₂) 5,3 durch Capsicum annuum. Dauer des Experiments 14 Wochen. (Viebrock, 1988)

long been debated. *Viebrock* (1988) found P depletion profiles in soil around VA-mycorrhizal root systems to be much wider than in non-mycorrhizal root systems, as shown in Fig. 8. Measurements of the amount of hyphae in the soil adjacent to the root surface revealed hyphae lengths of up to 1000 cm per g soil. At distances of 40 mm from the root 10 cm hyphae per g soil were still found. It can thus be concluded, that the efficiency of VA-mycorrhiza in acquiring P is largely due to the geometry of the hyphal system. In addition, chemical or enzymatic mechanisms may also be involved in P acquisition by mycorrhizae.

Acknowledgement

The authors thank Prof. *Colin J. Asher* and *David G. Edwards*, The University of Queensland, Australia, for their valuable comments. Financial support by the *Deutsche Forschungsgemeinschaft* is gratefully acknowledged.

References

- Barber, S.A.* (1984): Soil Nutrient Bioavailability. John Wiley, New York.
- Barracough, P.B.* (1986): The growth and activity of winter wheat roots in the field: nutrient inflows of high yielding crops. *J. Agric. Sci.* 106, 53-59.
- Bekele, T.; B.J. Cino; B.A. Ehlert; A.A. van der Maas and A. van Diest* (1983): An evaluation of plant-borne factors promoting the solubilization of alkaline rock phosphates. *Plant Soil* 75, 361-378.
- Bhat, K.K.S. and P.H. Nye* (1973): Diffusion of phosphate to plant roots in soil. I. Quantitative autoradiography of the depletion zone. *Plant Soil* 38, 161-175.
- Bhat, K.K.S. and P.H. Nye* (1974): Diffusion of phosphate to plant roots in soil. II. Uptake along the roots at different times and the effect of different levels of phosphorus. *Plant Soil* 41, 365-382.
- Claassen, N. and S.A. Barber* (1976): Simulation model for nutrient uptake from soil by a growing plant root system. *Agron. J.* 68, 961-964.
- Claassen, N.; L. Hendriks and A. Jungk* (1981 a): Erfassung der Mineralstoffverteilung im wurzelnahen Boden durch Autoradiographie. *Z. Pflanzenernaehr. Bodenk.* 144, 306-316.
- Claassen, N.; L. Hendriks and A. Jungk* (1981 b): Rubidiumverarmung des wurzelnahen Bodens durch Maispflanzen. *Z. Pflanzenernaehr. Bodenk.* 144, 533-545.
- Claassen, N. and A. Jungk* (1982): Kaliumdynamik im wurzelnahen Boden in Beziehung zur Kaliumaufnahme von Maispflanzen. *Z. Pflanzenernaehr. Bodenk.* 145, 513-525.
- Claassen, N. and A. Jungk* (1984): Bedeutung von Kaliumaufnahme, Wurzelwachstum und Wurzelhaaren für das Kaliumaneignungsvermögen verschiedener Pflanzenarten. *Z. Pflanzenernaehr. Bodenk.* 147, 276-289.
- Claassen, N.; K.M. Syring and A. Jungk* (1986): Verification of a mathematical model by simulating potassium uptake from soil. *Plant Soil* 95, 209-220.
- Claassen, N. and A. Jungk* (1987): Gradientenbildung und Nährstofftransport in der Rhizosphäre. *Mitteilgn. Dtsch. Bodenkundl. Gesellsch.* 53, 375-380.
- Föhse, D.* (1985): Die Bedeutung von Wurzeleigenschaften für das Phosphataneignungsvermögen verschiedener Pflanzenarten. Ph. D. Thesis Univ. Göttingen.
- Föhse, D. and A. Jungk* (1983): Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. *Plant Soil* 74, 359-368.
- Föhse, D.; N. Claassen and A. Jungk* (1988): Phosphorus efficiency of plants. 1. External and internal P requirements and P uptake efficiency of different plant species. *Plant Soil* 110, 101-109.
- Gahoonia, T.S.* (1987): Phosphate availability as influenced by root induced changes of soil pH. Ph. D. Thesis, Göttingen.
- Hedley, M.J.; R.E. White and P.H. Nye* (1982): Plant induced changes in the rhizosphere of rape seedlings. III. Changes in L value, soil phosphate fractions and phosphatase activity. *New Phytol.* 91, 45-56.
- Hendriks, L.; N. Claassen and A. Jungk* (1981): Phosphatverarmung des wurzelnahen Bodens und Phosphataufnahme von Mais. *Z. Pflanzenernaehr. Bodenk.* 144, 486-499.
- Jost, W.* (1952): Diffusion in Solids, Liquids, Gases. Academic Press, New York.
- Jungk, A.; N. Claassen and R. Kuchenbuch* (1982): Potassium depletion of the soil-root interface in relation to soil parameters and root properties. in: Scaife, A. (Ed.) *Proc. 9th Internat. Plant Nutr. Coll.* CAB.
- Kaselowsky, J.* (1985): Einfluß mehrjährig gestaffelter Phosphatdüngergaben auf die Phosphatdynamik im wurzelnahen Boden. Diploma Thesis, Univ. Göttingen.
- Kuchenbuch, R.* (1983): Die Bedeutung von Ionenaustauschprozessen im wurzelnahen Boden für die Pflanzenverfügbarkeit von Kalium. Ph. D. Thesis Göttingen.
- Kuchenbuch, R. and A. Jungk* (1982): A method for determining concentration profiles at the soil-root interface by thin slicing rhizosphere soil. *Plant Soil* 68, 391-394.
- Kuchenbuch, R.; N. Claassen and A. Jungk* (1986): Potassium availability in relation to soil moisture. I. Effect of soil moisture on potassium diffusion, root growth and potassium uptake of onion plants. *Plant Soil* 95, 221-231.
- Kuchenbuch, R.; N. Claassen and A. Jungk* (1986): Potassium availability in relation to soil moisture. II. Calculations by means of a mathematical simulation model. *Plant Soil* 95, 233-243.
- Lewis, D.G. and J.P. Quirk* (1967): Phosphate diffusion in soil and uptake by plants. III. ³¹P-movement and uptake by plants as indicated by ³²P-autoradiography. *Plant Soil* 27, 445-453.
- Müller, R.* (1988): Bedeutung des Wurzelwachstums für die Phosphater-nährung von Winterweizen, Wintergerste und Zuckerrüben. Ph. D. Thesis Göttingen.
- Nye, P.H.* (1966): The measurement and mechanism of ion diffusion in soil. I. The relation between self-diffusion and bulk diffusion. *J. Soil Sci.* 17, 16-23.
- Nye, P.H. and P.B. Tinker* (1977): Solute Movement in the soil-root system. *Studies in Ecology*, Blackwell Scientif. Publ. Oxford.
- Seggewiss, B. and A. Jungk* (1988): Einfluß der Kaliumdynamik im wurzelnahen Boden auf die Magnesiumaufnahme von Pflanzen. *Z. Pflanzenernaehr. Bodenk.* 151, 91-96.
- Tarafdar, J.C. and N. Claassen* (1988): Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatases produced by plant roots and microorganisms. *Biol. Fertil. Soils* 5, 308-312.
- Tarafdar, J.C. and A. Jungk* (1987): Phosphatase activity in the rhizosphere and its relation to the depletion of soil organic phosphorus. *Biol. Fertil. Soils* 3, 199-204.
- Viebrock, H.* (1988): Ursachen der Erhöhung des Phosphat-Aneignungsvermögens von Pflanzen durch VA-Mykorrhiza. Ph. D. Thesis, Göttingen.
- de Willigen, P. and M. van Noordwijk* (1987): Roots, plant production and nutrient use efficiency. Ph. D. Thesis, Wageningen.