FUNDAMENTALS OF SOIL-PLANT INTERACTIONS AS DERIVED FROM NUTRIENT DIFFUSION IN SOIL, UPTAKE KINETICS AND MORPHOLOGY OF ROOTS

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INTRODUCTION

The soil-root system comprises the root and the soil which is influenced by its activity. It is the site where the plant interacts with the soil. To understand this system with respect to the mineral nutrition of plants a process oriented approach has been used in this paper.

Soil nutrient ions have to be transported to the root surface in order to be taken up. For conservation of mass this transport through the soil has to be equal to the influx into the root (mol per cm^2 root surface area or per cm root length and per second). Therefore those factors and processes that affect nutrient transport in soil will be relevant for the mineral nutrition of plants. This also includes root exudates, uptake characteristics and morphological properties of the root, as well as the size of the root system.

MECHANISMS OF NUTRIENT TRANSPORT IN SOIL

In an already classical paper, Barber (1962) established that nutrient transport to the root surface proceeds by mass flow, F_M, and by diffusion, F_D, as defined by Eq. [1] and [2].

$$F_M = v \, C_l \qquad\qquad [1]$$
$$F_D = -D_e A (dC/dx) \qquad\qquad [2]$$

where v is the flux of water to the root, $cm^3 cm^{-2} s^{-1}$, C_l the concentration in soil solution, $mol \, cm^{-3}$, D_e the effective diffusion coefficient, $cm^2 s^{-1}$, A the cross sectional area of diffusion, cm^2, C the concentration of diffusible nutrient in soil, $mol \, cm^{-3}$ of soil, and x distance, cm, dC/dx is the concentration gradient. If diffusion only occurs in the solution phase, as has been shown for many cases (Rowell et al., 1967; Vaidyanathan et al., 1968) D_e is given by Eq. [3] (Nye, 1966)

$$D_e = D_l \, \theta \, f \, / \, b \qquad\qquad [3]$$

where D_l is the diffusion coefficient in water, θ the volumetric water content of the soil, cm^3/cm^3, f is the impedance factor, which is related to θ (Barraclough and Tinker, 1981) and b is the buffer power given by dC/dC_l.

Mass flow and diffusion occur simultaneously and are additive. The significance of them for P, K, Ca and Mg is shown for high yielding fields from Germany in Table 1. It can be seen that mass flow supplied only 1 to 3% of P and 1 to 14% of K uptake. Therefore the concentration of P and K at the root surface was decreased and the resulting concentration gradient caused the flow by diffusion which supplied the remaining 99 to 97% of P and 99 to 86% of K uptake. Mass flow moved 7 to 14 times more Ca as was taken up inducing a concentration increase at the root surface. For Mg mass flow and uptake was of similar size.

Measurements by Hendriks and Jungk (1981) on 12 different fields showed that the P concentration in the rhizosphere of wheat was generally

Table 1: The significance of transport by mass flow for the nutrition of high yielding crops on some sites in Germany. Soils derived from loess.

Site[1]	Crop	Yield	Soil sol. conc. mg/l				Transport[2] by massflow as % of uptake			
		t/ha	P	K	Ca	Mg	P	K	Ca	Mg
1	Wheat	8.8	0.40	3.5	113	6.5	3	2	848	115
2	Wheat	8.6	0.10	1.1	97	7.2	1	1	728	127
3	Wheat	8.6	0.17	15.3	92	9.3	1	10	690	164
4	Sugar beat	51.5	0.04	12.1	263	9.4	1	14	1481	94
5	Sugar beat	62.7	0.21	12.1	263	9.4	2	13	1169	78

(1)Site 1 = Oesselse (K-0, 86); 2 = Klein Ilde (K-0, 86); 3 = Klein Ilde (K-240, 86); 4 = Dinklar (P-0, 87); 5 = Dinklar (P-500, 87).
(2)Transport by mass flow was calculated from soil solution concentration and a transpired quantity of water of 300 l/m^2 for wheat and 400 l/m^2 for sugar beat.
Total uptake in kg/ha was: P 24 to 46; K 310 to 480; Ca 40 to 90; Mg 17 to 48.

lower (about 20%) and that of Ca higher (about 25%) than that of the remaining soil. More detailed studies with quantitative autoradiography (Claassen et al., 1981a) or a thin slicing technique (Kuchenbuch and Jungk, 1982) enable to draw the concentration profile of a nutrient in the rhizosphere. As an example, Fig. 1 shows that the decrease of P concentration is strongest at the root surface and extends to only 1.8 and 2.7 mm for maize and rape respectively. The wider depletion zone of rape is related to its longer root hairs. Whenever diffusion is the main transport mechanism a depletion, like shown in Fig. 1, will be observed, the extention of it will be a function of the mobility of the ion in soil which is expressed by the effective diffusion coeffcient. Claassen et al. (1981b) showed that the depletion of Rb (as a tracer for K) extendet 5 mm out from the root surface after only 4 days of uptake. Potassium usually has a lower buffer power than P and as a result its mobility is higher (see Eq. [3]).

The results of Table 1 furthermore show that nutrient transport by diffusion is much more efficient than by mass flow. A soil solution concentration of 0.1 mg P/l or 1.1 mg K/l was enough for diffusion to supply 99% of the plants demand. For the same supply mass flow would have needed about 10 mg P/l and 110 mg K/l. Therefore when soil nutrient content is low, but sufficient for maximum growth, diffusion will be the main transport mechanism.

UPTAKE CHARACTERISTICS OF THE ROOT

Physiological and morphological properties of a root influence its efficiency to absorb nutrients from soil. The relationship between influx, I_n, and concentration, C_l, Fig. 2, can be described by a modified Michaelis Menten kinetics (Nielsen, 1972). The necessary parameters are I_{max}, maximum influx, C_{lmin}, minimum concentration at which $I_n = 0$ and K_m the Michaelis constant, i.e. the difference between the concentration at which $I_n = ½ I_{max}$ and C_{lmin}. The uptake isotherme is then described by Eq. [4]

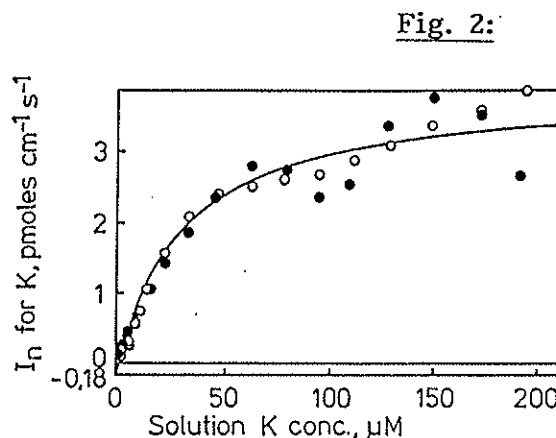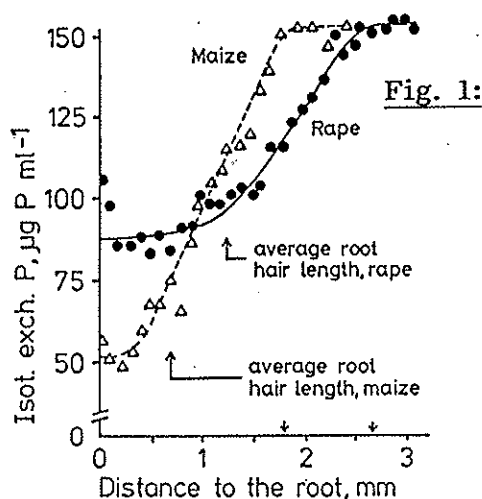$$I_n = I_{max} (C_l - C_{lmin}) / (K_m + C_l - C_{lmin}) \qquad [4]$$

Fig. 1: Phosphate distribution around 5 days old maize and rape roots
(Hendriks et al., 1981)

Fig. 2: Potassium uptake isotherm for 18 days old maize plants. Points are measured values and the line calculated with Eq. [4], I_{max} = 4 pmol $cm^{-1}s^{-1}$ K_m = 28 µM and C_{lmin} = 1.3 µM (Claassen and Barber, 1974)

A high I_{max} and low K_m value means a high I_n at low concentration, enabling the root to decrease soil solution concentration at the root surface to low values creating steep concentration gradients and thereby a high flux by diffusion towards the root.

Root radius, r_0, also affects the concentration gradient in soil solution, as can be derived from a modified equation of Barraclough (1986)

$$\Delta C_l = \overline{C_l} - C_{lo} = - \frac{I_{nA}\ r_0}{2\ D_l\ \theta\ f}\ (1 - \frac{2}{1-(r_0/r_1)^2}\ \ln \frac{r_1}{r_0})\ \ \ [5]$$

ΔC_l is the concentration difference between the average soil solution concentration, $\overline{C_l}$, and the concentration at the root surface C_{lo}. The significance of r_0 becomes clear when comparing nutrient uptake by a root of r_0 = 0.01 cm and a root hair of r_0 = 0.0005 cm. Taking a ΔC_l of 1 nmol P/cm^3 and r_1 the half distance between roots of 0.2 cm, D_l = $0.89x10^{-5}$ cm^2s^{-1}, θ = 0.25, and f = 0.23 I_{nA} (mol s^{-1} per cm^2 root surface area) for the root would be $2.0x10^{-14}$ and for the root hair $18.6.x10^{-14}$. Since D_e was the same for the root and root hair, the higher I_{nA} and therefore higher flux by diffusion for the root hair was due to a higher concentration gradient, Eq. [2]. Root hairs or mycorrhizal hyphae are therefore much more efficient to absorb P from soils of low P content than roots.

MODELLING NUTRIENT UPTAKE FROM SOIL

In previous sections nutrient transport in soil and the concentration dependence of nutrient influx were treated separatly. Mathematical modelling allows to put them together, simulating the functioning of the soil-plant system. It thereby becomes possible to test whether our perception of the system is adequate to explain nutrient uptake from soil.

The simulation models used here are based on:

1). Nutrient transport through the soil to the root surface by mass flow and diffusion, Eq. [1] and [2]. The two processes are additive.

2). The inflow of nutrients into the root follows Michaelis-Menten kinetic, Eq. [4].

For mass conservation the processes of transport and inflow are equated in the model; thereby the connection of soil and plant properties is obtained. The model also accounts for competition for nutrients of neighboring roots but not for chemical mobilization of nutrients. Details on simulation models with or without root hairs can be found in Nye and Marriott (1969), Claassen and Barber (1976), Cushman (1979), Itho and Barber (1983), Claassen et al. (1986), Claassen (1989).

The models presented above were applied to results of pot and field experiments. Figure 3a shows that calculated and actual K uptake of maize at six very different levels of K availability (3 soils x 2 K levels) are quite similar. The same holds for the P influx of seven plant species growing at several P levels of one soil (Fig. 3b). The correspondence of measured and calculated P influx was only achieved after including root hairs in the simulation model. Root hairs are of major importance when the mobility of a nutrient in soil is low, as is the case for P at low soil supply (see also Fig. 1).
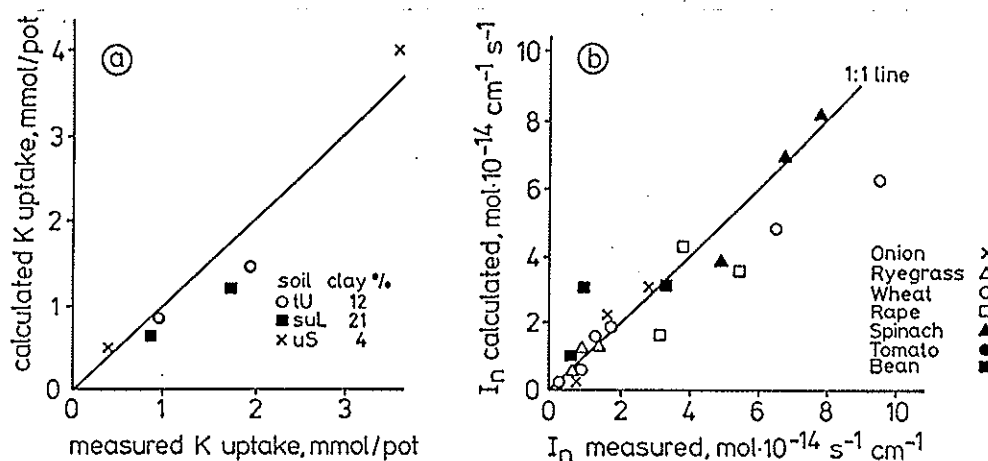

Fig. 3: Comparison of measured and by a simulation model calculated a) K uptake (Claassen et al., 1986) and b) P-influx (I_n) including the contribution by root hairs (Foehse et al., 1990)

The fact that these models could explain large differences in P or K uptake indicates that the perception of the system is realistic and for the cases studied, chemical mobilization of nutrients was absent or of minor significance. This is not always the case as will be shown later.

Mathematical modelling allows to asses the significance of soil and plant parameters by changing them systematically. In this way it can be shown that soil solution concentration, C_{li}, is of major significance for nutrient uptake, followed by soil water content, θ, and the impedance factor, f, while the buffer power, b, has only a minor influence on uptake. The significance of b increases if strong competition for nutrients among roots exists. The reason for the above findings is that nutrient diffusion in soil only occurs in the liquid phase. Of the plant parameters maximum influx, I_{max}, is the one of major significance followed by root radius, as discussed earlier, and the Michaelis constant, K_m.

MOBILIZATION OF NUTRIENTS BY ROOT EXUDATES

Since nutrients move in the liquid phase only root exudates will mobilize nutrients if they cause ions bound to the solid phase to go into solution. Thereby soil solution concentration is increased which will

enhance nutrient transport to the root as was shown by model calculations.

The chemical mobilization of micronutrients, more specifically, Fe, by root exudates is well documented and the substances involved identified (Marschner et al., 1989).

Chemical mobilization of macronutrients, mainly P, has been postulated many times. This mobilization has often been associated to root induced pH changes in the rhizosphere, as shown in Fig. 4 (Gahoonia, 1987). The
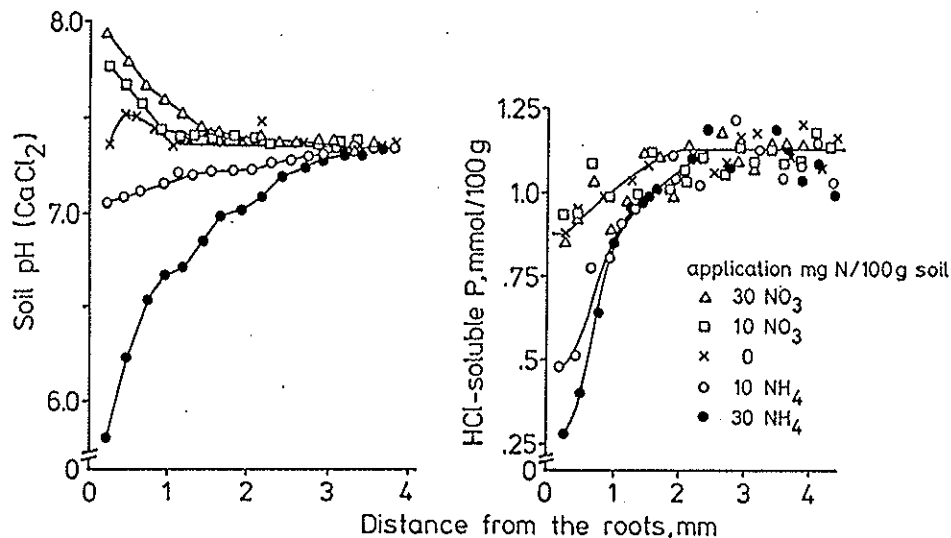

Fig. 4: pH change and P depletion in the rhizosphere of ryegrass 10 days old as influenced by NH_4-N and NO_3-N nutrition (silt loam soil from loess) (Gahoonia, 1987)

observed decrease of pH in the rhizosphere due to NH_4-N nutrition, even a small one (10 mg NH_4-N/100 g) is associated with a large depletion of P at the root surface. When, in another experiment, the soil was acidified artifically with H_2SO_4, P depletion at the root surface was also increased, but to a much smaller extent, indicating that other principles than the pH also influenced P mobilization of NH_4-fed plants. The same can be shown for maize in a pot experiment where the rhizospheric soil pH was influenced both by the N-form and by the pH of the bulk soil (Fig. 5). It shows that in this soil, of mainly Fe and Al phosphates (a fossile oxisol), the pH of the rhizosphere had almost no effect on P influx, i.e. on P transport to the root, while at the same pH NH_4-fed plants showed a 50 to 100% higher influx. Therefore plants absorbing NH_4-N must have excreted some substances that increased P concentration in soil solution resulting in higher transport to the root. The nature of these substances is not known.

The significance P mobilization may have for field grown crops illustrates Fig. 6. It can be seen by model calculations that included root hairs but, as was discussed earlier, did not account for chemical mobilization only explained 25% of the actual uptake on the low P plots. The remaining 75% would therefore result from chemical mobilization of P. Even though the effect of P mobilization is large the needed increase in soil solution concentration may be small since it occurs in the zone of P depletion shown in Fig. 1 and furthermore if P uptake is largly by root hairs of small radius (see Eq. 5). It may therefore be difficult to be able to measure that effect on soil solution concentration. The agent causing this increased P transport to the root needs more research.
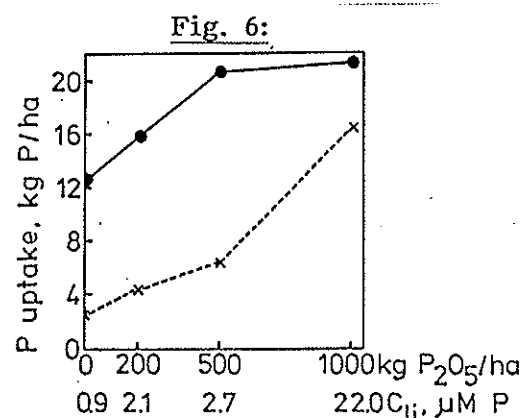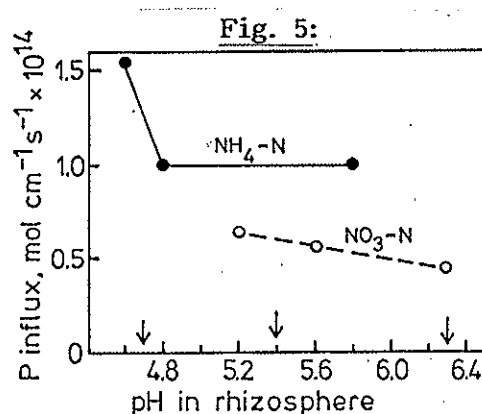
Fig. 5: Phosphate influx of maize as influenced by the pH in the rhizo-
sphere and by NH4- or NO3-N nutrition. ↓= pH of bulk soil
Fig. 6: Phosphate uptake by sugar beet in July at different P fertilizer
rates (soil C_{li} = solution concentrations). ●= measured, x = calculated
by a simulation model including root hairs

OUTLOOK

Among the processes occurring in the soil-plant system transport of
nutrients and factors affecting it are best understood. It is possible to
describe it by mathematical simulation models. On the orther hand
substances excreted by plant roots that mobilize nutrients are identified
in part only and the mode of action of them in the soil is often not
understood. These aspects need more research efforts.

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