

# Phosphorus uptake of maize as affected by ammonium and nitrate nitrogen - Measurements and model calculations -

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## Summary - Zusammenfassung

Phosphorus uptake is often enhanced by ammonium compared to nitrate nitrogen nutrition of plants. A decrease of pH at the soil-root interface is generally assumed as the cause. However, an alteration of root growth and the mobilization of P by processes other than net release of protons induced by the source of nitrogen may also be considered. To study these alternatives a pot experiment was conducted with maize using a fossil Oxisol high in Fe/Al-P with low soil solution P concentration. Three levels of phosphate (0, 50, 200 mg P kg<sup>-1</sup>) in combination with either ammonium or nitrate nitrogen (100 mg N kg<sup>-1</sup>) were applied. Plants were harvested 7 and 21 d after sowing, P uptake measured and root and shoot growth determined. To assess the importance of factors involved in the P transfer from soil into plants, calculations were made using a model of Barber and Claassen. In the treatments with no and low P supply NH<sub>4</sub>-N compared to NO<sub>3</sub>-N nutrition increased the growth of the plants by 25 % and their shoot P content by 38 % while their root growth increased by 6 % only. The rhizosphere pH decreased in the NH<sub>4</sub>-N treatments by 0.1 to 0.6 units as compared to the bulk soil while in the NO<sub>3</sub>-N treatments it increased by 0.1 to 0.5 units. These pH changes had a minor influence on P uptake only, as was demonstrated by artificially altering the soil pH to 4.7 and 6.3 respectively. At the same rhizosphere pH, however, P influx was doubled by the application of NH<sub>4</sub>-N compared to NO<sub>3</sub>-N. It is concluded that in this soil the enhancement of P uptake of maize plants after ammonium application cannot be attributed to the acidification of the rhizosphere but to effects mobilizing soil phosphate or increasing P uptake efficiency of roots. Model calculation showed that these effects accounted for 53 % of the P influx per unit root length in the NO<sub>3</sub>-N and 72 % in the NH<sub>4</sub>-N supplied plants if no P was applied. With high P application the respective figures were only 18 and 19 %.

## Phosphoraufnahme von Mais unter dem Einfluß von Ammonium- und Nitratstickstoff - Messungen und Modellrechnungen -

Die Phosphoraufnahme von Pflanzen wird durch die Ernährung mit Ammonium- gegenüber Nitratstickstoff gefördert. Als Ursache wird allgemein die Absenkung des pH-Wertes in der Grenzschicht von Boden und Wurzel angenommen. Denkbar ist jedoch auch eine Veränderung des Wurzelwachstums und chemische P-Mobilisierungsprozesse. Um diese Alternativen zu überprüfen wurde ein Gefäßversuch mit Mais in einem fossilen Oxisol mit hohem Gehalt an Fe/Al-Phosphat aber niedriger P-Konzentration der Bodenlösung untersucht. Der Boden erhielt 0, 50 bzw. 200 mg kg<sup>-1</sup> P sowie 100 mg kg<sup>-1</sup> NH<sub>4</sub>-N bzw. NO<sub>3</sub>-N. Pflanzen wurden nach 7 und 21 Tagen geerntet und ihre P-Aufnahme sowie das Wurzel- und Sproßwachstum gemessen. Um den Einfluß der beteiligten Faktoren abzuschätzen, wurde ein Rechenmodell von Barber und Claassen angewendet. Die Ergebnisse zeigen, daß ohne oder bei niedriger P-Gabe im Durchschnitt NH<sub>4</sub>-N- gegenüber NO<sub>3</sub>-N-Ernährung den Wuchs der Pflanzen um 25 % und ihre P-Aufnahme um 38 % erhöhte während das Wurzelwachstum nur um 6 % zunahm. Der Rhizosphären-pH-Wert sank während der Versuchszeit gegenüber dem wurzelfernen Boden nach NH<sub>4</sub>-Düngung um 0,1 bis 0,6 Einheiten ab, nach NO<sub>3</sub>-Düngung stieg er dagegen um 0,1 bis 0,5 Einheiten an. Diese pH-Änderungen hatten nur geringen Einfluß auf die P-Aufnahme, was durch die pH-Veränderungen (mittels H<sub>2</sub>SO<sub>4</sub> auf 4,7 bzw. NaHCO<sub>3</sub> auf 6,3) gezeigt wurde. Bei gleichem Rhizosphären-pH war der P-Influx bei NH<sub>4</sub>-N-Ernährung dagegen doppelt so groß wie bei NO<sub>3</sub>-N-Ernährung. Daraus wird der Schluß gezogen, daß die durch NH<sub>4</sub>-N-Ernährung der Pflanzen ausgelöste Förderung der P-Aufnahme in diesem Boden nicht der pH-Absenkung in der Wurzel-Boden-Grenzschicht, sondern anderen Mobilisierungsprozessen oder der Steigerung der P-Aufnahmeeffizienz der Wurzeln zuzuschreiben ist. Die Modellrechnung ergab, daß der P-Influx pro Einheit Wurzellänge zu 53 % bei NO<sub>3</sub>-N- und zu 72 % bei NH<sub>4</sub>-N-Ernährung von diesem P-mobilisierenden Effekt bestimmt wurde. Nach reichlicher P-Düngung betragen die entsprechenden Werte nur 18 und 19 % des gemessenen Influxes.

## Introduction

The transfer of phosphorus from soil into plants is the result of interactions between soil and plant which happens in a small cylinder of soil adjacent to plant roots (Jungk and Claassen, 1989). The basic processes of the P movement from soil to root are mass flow and diffusion. Influx into

the root is usually in agreement with Michaelis-Menten kinetics. Supply of a whole plant depends also on shoot and root growth as well as on the size and on morphological properties of the root system. These processes and factors and their interactions are now so well known that, in many cases, they can fairly be predicted by using the mechanistic mathematical model developed by Barber and Claassen

(Barber, 1984; Claassen, 1990). In case of low P availability, however, real P uptake of plants is often markedly higher than predicted by the model (Jungk et al., 1993). This indicates that plant induced P mobilizing processes, which are not allowed for in the model yet, may be important in plant P supply.

The source of nitrogen is one of the factors affecting P supply of arable crops. Phosphate uptake from soil is often enhanced when plants are supplied with ammonium instead of nitrate nitrogen (Miller, 1974). This effect is generally ascribed to the acidification of the rhizosphere caused by ammonium N nutrition (Riley and Barber, 1971; Marschner et al., 1986).

A lowered pH in the soil surrounding the roots would have two effects: (1) Increase the  $H_2PO_4^-/HPO_4^{2-}$ -ratio and thereby increase the phosphate ion that is preferentially absorbed by roots (Chen and Barber, 1990) and (2) increase the solubility of Ca-phosphates. In accordance with this hypothesis Riley and Barber (1971) found a close correlation between P concentration in soybean shoots and the pH of the soil adhering to their roots. Blair et al. (1971) observed that  $NH_4$ -N nutrition enhanced P uptake mainly in alkaline soil. Gahoonia et al. (1992), studying soil P release in the rhizosphere of ryegrass, found that, under  $NH_4$ -N nutrition, soil P depletion in the vicinity of roots was also correlated with the pH decrease in a calcareous Luvisol. However, using an Oxisol high in Fe/Al-P,  $NO_3$ -N nutrition favoured soil P release whereas  $NH_4$ -N did not. It may, therefore, be assumed that influences other than by protons are involved in the mobilization of soil P in the rhizosphere as the result of different nitrogen sources.

The aim of this work was to reconsider the role of the nitrogen source in P uptake of maize by quantifying its influence on root growth and on P influx per unit root. The main point was the question: Can differences in P influx caused by  $NH_4$ - or  $NO_3$ -N supply be explained by the accompanying changes of the rhizosphere pH or are other mechanisms responsible? For the experiment, the fossil Oxisol as also used by Gahoonia et al. (1992) was chosen because it was high in total and sorbed P and low in acid soluble P.

## Materials and Methods

In order to separate the pH effect of the N-form from the effect of the N-form on other P mobilizing processes similar pH values in the rhizosphere of plants supplied with  $NO_3$ -N or with  $NH_4$ -N are needed. This was achieved in a pot experiment with maize growing in a soil that had been adjusted to three different pH values. To assess the significance of chemical P mobilization by maize plants calculations were performed with a modified version of the Barber-Claassen model. It is based on nutrient transport from soil to root by mass flow and diffusion. Roots are assumed to function as a sink for P without any influence on the chemical environment of the rhizosphere except P concentration. Differences between calculated and actually measured P uptake can thus be ascribed to processes other than those included in the model.

## Pot experiment

Maize (*Zea mays* cv. Forla) was grown in a growth chamber in pots containing 2.7 kg of air dry soil moistened to 200 g water per kg. The growth chamber was maintained at 20 °C, a photosynthetic active radiation of 300  $\mu E \cdot m^{-2} \cdot s^{-1}$  and 80 % relative humidity during 16 h day and at 15 °C and 70 % relative humidity during 8 h night. The soil used was a low P fossil Oxisol from Lich in the Vogelsberg area, Germany, with a pH (0.01 M  $CaCl_2$ ) of 5.4. This pH value was (1) left unchanged or (2) decreased to 4.7 by adding  $H_2SO_4$   $kg^{-1}$  soil or (3) increased to 6.3 by adding  $NaHCO_3$   $kg^{-1}$  soil.  $NaHCO_3$  instead of  $CaCO_3$  was used to simulate the pH increase produced by plants that absorb more anions than cations, like  $NO_3$ -N supplied plants, and also to avoid the interference of Ca ions with the solubility of native or fertilizer P. Three P levels of 0, 50 or 200 mg P  $kg^{-1}$  were supplied as  $NaH_2PO_4$  and 100 mg N per kg soil either as  $Ca(NO_3)_2$  or as  $(NH_4)_2SO_4$  were given. To avoid nitrification of  $NH_4$ -N 5 mg Didin (Dicyandiamid) were applied per kg soil. The nitrification inhibitor was also applied to the  $NO_3$ - treatments. Only for the soil that was not fertilized with P all combinations of pH and N form were used while the 50 and 200 mg P per kg soil was kept at the original pH of 5.4 (see also Table 2).

All treatments received 50 mg K ( $K_2SO_4$ ), 40 mg Mg ( $MgSO_4$ ), 0.2 mg B ( $H_3BO_3$ ) and 0.1 mg Mo ( $(NH_4)_6Mo_7O_{24}$ ) per kg of soil.

The experiment was run with 4 replicates. One replicate with 8 plants per pot was harvested at 7 days and the remaining replicates with 4 plants per pot were harvested 21 days after sowing. The two harvests were necessary to calculate the P influx. At both harvests shoot dry weight, shoot P concentration and root length were determined. At the second harvest additional measurements were made of root radius,  $r_0$ , the root length density per volume of soil, which allows calculation of the half distance between roots,  $r_1$ , the pH in the rhizosphere and root hair length and density. Root surface area was calculated from length and average diameter of roots and root hairs.

## Plant and soil measurements

Shoots were dried and after wet digestion analysed for P (Kitson and Mellon, 1944). Root length, RL in cm, was measured by the method of Newman (1966) after washing the roots free of soil. Phosphorus influx,  $I_n$ , was calculated by equation 1 (Williams, 1948):

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

where U is total P content in the shoots, mol per plant, t is time, s, and the subscripts 1 and 2 refer to the first and the second harvest.

Root hair length and distribution was measured under a microscope at 50 fold magnification using the procedure outlined by Brewster et al. (1976).

Soil solution was obtained by the displacement procedure of Adams (1974) and P concentration in it was measured according to Murphy and Riley (1962). To characterize the P status of the soil the Ca-Acetate-Lactate (CAL) extraction of Schüller (1969) and water soluble P according to Van der Paauw and Sissingh (1971) was used. Soil pH was determined in 0.01 M  $CaCl_2$  in a soil/solution ratio 1/15. After the second harvest root segments with rhizosphere soil adhering to them were gently moved in a given volume of  $CaCl_2$  solution to wash off the soil. As many root segments were washed free of soil as were necessary to reach the soil/solution ratio of 1/15. The pH was measured in this soil suspension. Inorganic soil P was fractionated into acid soluble "Ca-P" and alkaline soluble "Fe/Al-P" by the method of Kurmies (1972).

## Model calculation

Phosphorus uptake was simulated by two mathematical models that are based on ion transport from soil to the root surface by mass flow and diffusion, and on Michaelis-Menten kinetics for uptake into the root. One of the models treats the root as a smooth cylinder (Claassen et al., 1986) while the other also includes root hairs as part of the absorbing root surface (Claassen, 1990). Soil and plant parameters needed for model calculation are listed below as well as their determination.

## Soil parameters

$C_{ii}$ , mol cm<sup>-3</sup>: Phosphorus concentration of soil solution at the beginning of the experiment. It was measured in the displaced soil solution as described by Adams (1974).

$b$ : The buffer power was calculated from  $\Delta C/\Delta C_1$  where  $\Delta C$  is the amount of P added (mol cm<sup>-3</sup> soil) and  $\Delta C_1$  is the corresponding increase in soil solution concentration (mol cm<sup>-3</sup> solution). In case of no P application,  $b$  was assumed to be equal to that of the P-50 treatment.

$D_e$ , cm<sup>2</sup> s<sup>-1</sup>: The effective diffusion coefficient. It was calculated from equation 2 (Nye, 1968).

$$D_e = D_1 \theta f / b \quad (\text{Eq. 2})$$

where  $D_1$  = diffusion coefficient in free solution (0.89 x 10<sup>-5</sup> cm<sup>2</sup> s<sup>-1</sup> at 25 °C),  $\theta$  = volumetric water content (maintained at 0.26 cm<sup>3</sup> cm<sup>-3</sup>) and  $f$  = the impedance factor, calculated after Barracough and Tinker (1981) ( $f = 0.99 \theta - 0.17$ ) which applies to rather heavy soils as the one used here.

## Plant parameters

$I_{max}$ , mol cm<sup>-2</sup> s<sup>-1</sup>: Maximum net influx. It was determined from the P influx measured at high P fertilization assuming that P concentration in soil solution was high enough not to limit P uptake. Since  $I_{max}$  was extrapolated for infinite concentration, the measured influx was increased by 10%. The  $I_{max}$  values initially determined per cm of root were divided by the root surface area per cm of root length to express  $I_{max}$  on a cm<sup>2</sup> basis, as required for calculations with the model. When root hairs were included in the model, their surface area per cm of root length was added to the surface area of the root cylinder.

$C_{imin}$ , mol cm<sup>-3</sup>: Soil solution concentration where net influx equals zero.

$K_m$ , mol cm<sup>-3</sup>: Michaelis constant, it is the difference between  $C_{imin}$  and the concentration where influx is half  $I_{max}$ . It was set at  $2 \times 10^{-10}$  mol cm<sup>-3</sup>, which is in the lower range of values found in the literature (Barber, 1984; Buhse, 1992). Choosing  $C_{imin}$  and  $K_m$  in the lower range means a high uptake efficiency at low P concentrations. The model will then calculate the maximum P influx possible for the soil. A higher measured than calculated P influx would then be an indicator of chemical P mobilization by the root.

$r_1$ , cm: Half average distance between adjacent roots. It is given approximately by  $1/\sqrt{(\pi RL_v)}$ , where  $RL_v$  is the root length density in soil, cm cm<sup>-3</sup>.

$v_0$ , cm<sup>3</sup> cm<sup>-2</sup> s<sup>-1</sup>: Water influx, was determined from the daily watering of the plants.

$r_0$ , cm: Root radius was calculated from root fresh weight (RFW) in g and RL in cm by  $r_0 = \text{RFW} / \sqrt{(\pi RL)}$ .

$k$ , s<sup>-1</sup>: Relative root growth rate. It is given by  $k = \ln(RL_2 / RL_1) / t_2 - t_1$ .

## Results

### Pot experiment

The soil used in this experiment is a fossil Oxisol. P fractions measured were: 685 mg P kg<sup>-1</sup> as Fe/Al phosphate and 354 mg kg<sup>-1</sup> as acid soluble phosphate. The clay content was 50% and the pH (CaCl<sub>2</sub>) 5.4. Table 1 shows that decreasing the pH of the soil to 4.7 had no effect on P soil solution concentration, while an increase to 6.3 caused an increase in soil solution P concentration from 0.19 to 0.28 μmol L<sup>-1</sup>. Water extractable P (P-H<sub>2</sub>O) behaved similarly while the CAL-extractable P reacted only slightly to changes in soil pH. These results show that a pH increase tends to improve P availability in this soil. Fertilizing the soil increased P soil solution concentration as well as P-CAL and P-H<sub>2</sub>O (Table 1).

Table 1: Influence of soil pH (0.01 M CaCl<sub>2</sub>) and P fertilization on P soil solution concentration,  $C_{ii}$ , and soil test values

Tabelle 1: Wirkung des pH-Wertes des Bodens (0.01 M CaCl<sub>2</sub>) und der P-Düngung auf die P-Konzentration der Bodenlösung sowie den P<sub>CAL</sub>- und P<sub>H<sub>2</sub>O</sub>-Wert des Bodens

pH	P fert. mg kg <sup>-1</sup>	$C_{ii}$ μmol L <sup>-1</sup>	P-CAL mg kg <sup>-1</sup>	P-H <sub>2</sub> O mg kg <sup>-1</sup>
4.7	0	0.19	5.1	0.34
5.4	0	0.19	6.1	0.40
6.3	0	0.28	6.6	0.55
5.4	50	0.31	10.1	1.06
5.4	200	10.29	37.8	3.95

Table 2: Influence of N form on plant growth and shoot P concentration at three soil pH values and three P levels in soil. Results are for the second harvest

Tabelle 2: Wirkung der N-Form auf das Wachstum von Sproß und Wurzel sowie den P-Gehalt des Sprosses der Maispflanzen bei drei pH-Werten und drei P-Düngungsstufen des Bodens. Ergebnisse der zweiten Ernte

pH	N form	P fert. mg kg <sup>-1</sup>	Shoot d. m. g plant <sup>-1</sup>	Shoot P conc. mg g <sup>-1</sup>	Root length m plant <sup>-1</sup>
4.7	NO <sub>3</sub> <sup>-</sup>	0	0.80 c	1.3 d	87 a
4.7	NH <sub>4</sub> <sup>+</sup>	0	1.00 c	1.9 cd	93 a
5.4	NO <sub>3</sub> <sup>-</sup>	0	0.81 c	1.2 d	111 a
5.4	NH <sub>4</sub> <sup>+</sup>	0	0.99 c	1.6 d	123 a
6.3	NO <sub>3</sub> <sup>-</sup>	0	0.80 c	1.2 d	96 a
6.3	NH <sub>4</sub> <sup>+</sup>	0	0.89 c	1.6 cd	113 a
5.4	NO <sub>3</sub> <sup>-</sup>	50	1.08 bc	1.6 d	122 a
5.4	NH <sub>4</sub> <sup>+</sup>	50	1.56 a	2.2 bc	107 a
5.4	NO <sub>3</sub> <sup>-</sup>	200	1.58 a	2.8 b	105 a
5.4	NH <sub>4</sub> <sup>+</sup>	200	1.46 ab	4.5 a	86 a

Differences between figures are significant (Tukey 0.05) if followed by different characters

Shoot yield (Table 2), on the soil without P application, did not respond when soil P was altered between 4.7 and 6.3. However, NH<sub>4</sub>-N nutrition was superior to NO<sub>3</sub>-N in combination with no P and particularly with the medium P

level. The maximum yield of 1.6 per plant was achieved with both N sources but in combination with  $\text{NO}_3\text{-N}$  a much higher P application was necessary than with  $\text{NH}_4\text{-N}$ .

Root length per plant (Table 2) varied from 86 to 123 m per plant. On the no P soil root length was always somewhat higher in  $\text{NH}_4\text{-N}$  than in  $\text{NO}_3\text{-N}$  supplied plants. This trend reversed with P application, i.e. root length was higher for the  $\text{NO}_3\text{-N}$  supplied plants. Shoot P concentration (Table 2) varied from 1.2 to 4.5  $\text{mg g}^{-1}$  and showed a similar pattern as the yield, i.e. no influence of soil pH but a markedly higher P concentration in  $\text{NH}_4\text{-}$  compared to  $\text{NO}_3\text{-N}$  supplied plants.

Total P uptake of plants on the no-P soil is shown in Fig. 1. It can be seen that bulk soil pH had no influence on P uptake of  $\text{NO}_3\text{-N}$  treated plants while supplying plants with  $\text{NH}_4\text{-N}$  increased P uptake by 40 % at pH 6.3 to 80 % at pH 4.7.

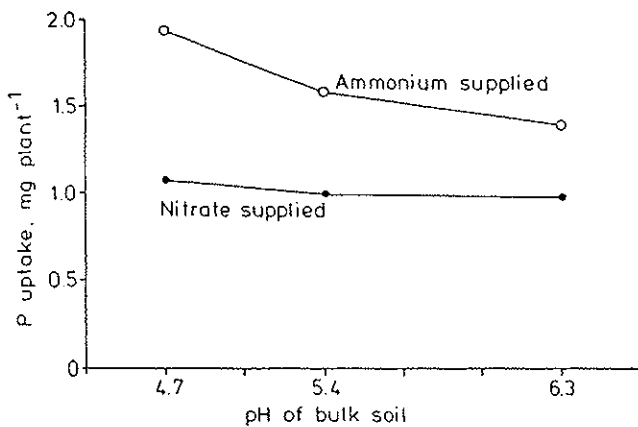


Figure 1: Phosphorus uptake of maize plants supplied with either  $\text{NH}_4\text{-}$  or  $\text{NO}_3\text{-}$ nitrogen in relation to bulk soil pH ( $\text{CaCl}_2$ )

Abbildung 1: Phosphataufnahme von  $\text{NH}_4\text{-}$  bzw.  $\text{NO}_3\text{-}$ ernährten Maispflanzen in Beziehung zum pH-Wert des Durchschnittsbodens

While Table 2 gave the absolute values of shoot dry matter and root length, Fig. 2 shows root/shoot ratio as a function of P concentration in the shoot. The root/shoot ratio was about 13  $\text{cm mg}^{-1}$  at a shoot P concentration of 1.3  $\text{mg g}^{-1}$  and decreased to about half that value towards higher shoot P concentrations. This relationship was the same for  $\text{NO}_3$  and  $\text{NH}_4$  supplied plants, i.e. the N source did not influence root/shoot ratio by itself but by influencing the P status of the plants.

Figure 3 relates P influx on the no-P soil to pH as measured in the rhizosphere. These pH values always deviated from bulk soil pH which is indicated by arrows. It can be seen that  $\text{NH}_4\text{-N}$  supplied plants decreased and  $\text{NO}_3\text{-N}$  supplied plants increased the pH of the rhizosphere. The P influx of  $\text{NO}_3\text{-N}$  supplied plants decreased from  $0.64 \times 10^{-14}$  to  $0.43 \times 10^{-14}$   $\text{mol cm}^{-1} \text{ s}^{-1}$  when the rhizosphere pH increased from 5.2 to 6.4. The respective influx of the  $\text{NH}_4\text{-N}$  treatments varied between  $1.6 \times 10^{-14}$  and  $1.1 \times 10^{-14}$   $\text{mol cm}^{-1} \text{ s}^{-1}$  while the rhizosphere pH changed from

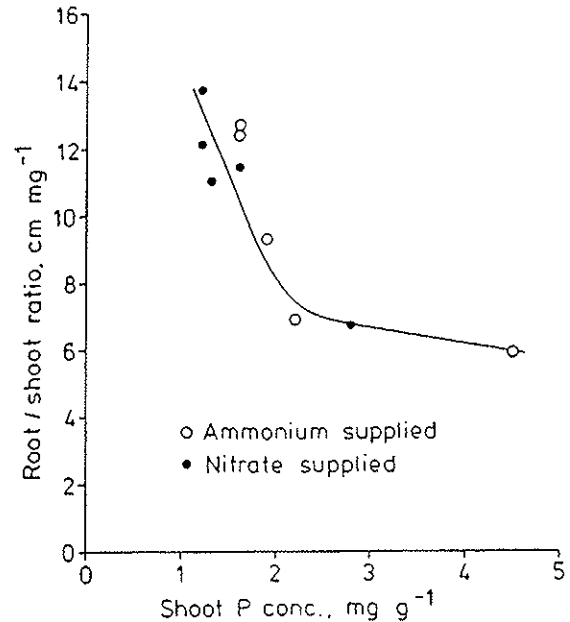


Figure 2: Root/shoot ratio of maize plants supplied with either  $\text{NH}_4\text{-}$  or  $\text{NO}_3\text{-}$ nitrogen as a function of shoot P concentration

Abbildung 2: Wurzel/Sproß-Verhältnis von  $\text{NH}_4\text{-}$  bzw.  $\text{NO}_3\text{-}$ ernährten Maispflanzen als Funktion der P-Konzentration des Sprosses

4.6 to 5.8. It can be seen that with increasing rhizosphere pH the influx tended to decrease but that at any pH value  $\text{NH}_4\text{-N}$  supplied plants had a P influx about twice that of the  $\text{NO}_3\text{-N}$  treated plants. This higher P influx is, therefore, not the consequence of a decrease of pH in the rhizosphere caused by  $\text{NH}_4\text{-N}$  nutrition.

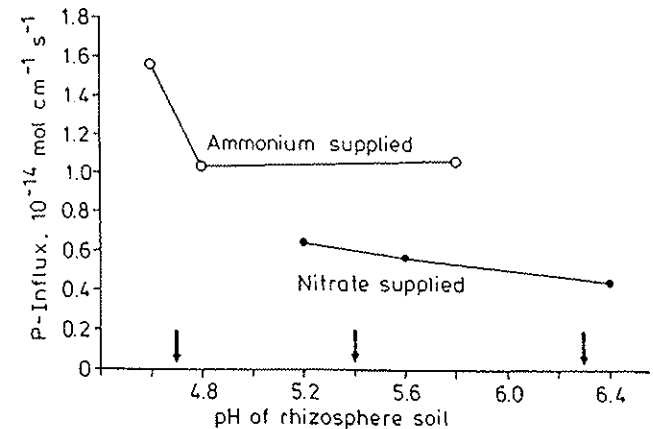


Figure 3: Phosphorus influx into maize roots supplied with either  $\text{NH}_4\text{-}$  or  $\text{NO}_3\text{-}$ nitrogen in relation to rhizosphere pH ( $\text{CaCl}_2$ ). Arrows indicate the three bulk soil pH levels when maize was planted. The original soil pH of 5.4 was either left unchanged or lowered to 4.7 by adding  $\text{H}_2\text{SO}_4$  or raised to 6.3 by adding  $\text{NaHCO}_3$

Abbildung 3: Phosphor-Influx in Maiswurzeln nach  $\text{NH}_4\text{-}$  bzw.  $\text{NO}_3\text{-}$ Düngung in Beziehung zum pH-Wert des wurzelnahen Bodens. Die Pfeile bezeichnen die pH-Werte des Bodens zu Versuchsbeginn. Der ursprüngliche pH-Wert von 5,4 wurde entweder belassen oder durch  $\text{H}_2\text{SO}_4$  auf 4,7 abgesenkt bzw. durch  $\text{NaHCO}_3$  auf 6,3 angehoben

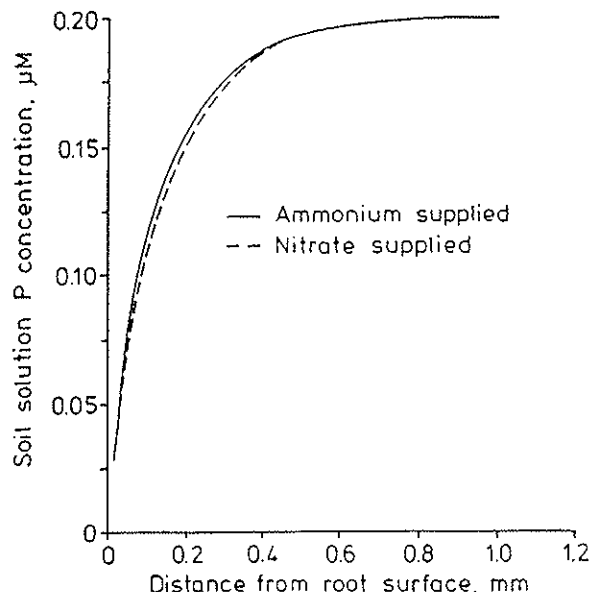
**Model calculations**

The parameters used in the model calculations are listed in Table 3. P application increased P soil solution concentration, decreased the buffer power and thereby increased the effective diffusion coefficient. The source of N affected the maximum influx, which was almost twice as large in the NH<sub>4</sub>-N compared to the NO<sub>3</sub>-N treated plants. The remaining parameters, including length and density of root hairs, were similar for all treatments.

On the no-P soil the model omitting root hairs indicated (Table 4) an influx of  $0.1 \times 10^{-14} \text{ mol cm}^{-1} \text{ s}^{-1}$  for both the NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> treated plants, which is only 18 and 10 % of the measured influx. When root hairs were included in the model calculated influx increased by a factor of almost 3 and reached up to 47 % of measured influx for NO<sub>3</sub>-N but only 28 % for NH<sub>4</sub>-N treated plants. It can be seen that the difference in I<sub>max</sub> of NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>-N treated plants had no effect on the calculated influx on the unfertilized soil.

On the soil fertilized with P the model predicted up to about 80 % of the influx when root hairs are included in the model. In this case it can be observed that the higher I<sub>max</sub> value of NH<sub>4</sub><sup>+</sup> treated plants is effective in increasing the calculated influx from  $2.9 \times 10^{-14}$  to  $5.3 \times 10^{-14} \text{ mol cm}^{-1} \text{ s}^{-1}$ .

The P concentration profiles around roots supplied with NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>-N after 14 days of uptake on the no-P soil are shown in Fig. 4 as calculated by the model which includes root hairs. The curves for NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>-N sup-



**Figure 4:** Calculated P depletion profiles of the soil around maize roots supplied with either NH<sub>4</sub><sup>-</sup> or NO<sub>3</sub>-nitrogen and no P added  
**Abbildung 4:** Durch Modellrechnung ermittelte P-Verarmungsprofile der Bodenlösung im wurzelnahen Boden von Maiswurzeln bei NH<sub>4</sub><sup>-</sup> bzw. NO<sub>3</sub>-N-Düngung ohne P-Gabe

plied roots are very similar as could be expected from the similarity of the calculated influx. The depletion zone extended to about 0.5 mm and thus remained within the

**Table 3:** Parameters used in the model calculations with root hairs either included (+) or omitted (-)

**Tabelle 3:** Parameter für die Modellrechnung der P-Aufnahme, wobei die Wurzelhaare entweder berücksichtigt (+) oder nicht berücksichtigt (-) wurden

Treatment		C <sub>ii</sub>	D <sub>e</sub>	b	v <sub>o</sub>	I <sub>max</sub> root hairs		r <sub>1</sub>	k
P	N form					-	+		
mg kg <sup>-1</sup>									
0	NO <sub>3</sub> <sup>-</sup>	0.19	3.0	6764	1.6	5.1	2.5	0.13	2.8
0	NH <sub>4</sub> <sup>+</sup>	0.19	3.0	6764	1.7	9.6	4.8	0.12	2.9
200	NO <sub>3</sub> <sup>-</sup>	10.3	24.7	815	2.1	5.1	2.5	0.13	2.7
200	NH <sub>4</sub> <sup>+</sup>	10.3	24.7	815	2.2	9.6	4.8	0.14	2.7

The same for all treatments: r<sub>o</sub> = 0.012 cm; K<sub>m</sub> =  $2 \cdot 10^{-10} \text{ mol cm}^{-3}$ ; C<sub>imin</sub> = 0.0 mol cm<sup>-3</sup>; root hair length = 23.9 cm cm<sup>-1</sup> root; number of root hairs = 544 cm<sup>-1</sup> root.

Units: C<sub>ii</sub> [10<sup>-9</sup> mol cm<sup>-3</sup>], D<sub>e</sub> [10<sup>-11</sup> cm<sup>2</sup> s<sup>-1</sup>], v<sub>o</sub> [10<sup>-6</sup> cm<sup>3</sup> cm<sup>-2</sup> s<sup>-1</sup>], I<sub>max</sub> [10<sup>-13</sup> mol cm<sup>-2</sup> s<sup>-1</sup>], r<sub>1</sub> [cm], k [10<sup>-6</sup> s<sup>-1</sup>].

**Table 4:** Comparison of measured and calculated P influx into maize roots (10<sup>-14</sup> mol cm<sup>-1</sup> s<sup>-1</sup>)

**Tabelle 4:** Vergleich von gemessenem und durch Modellrechnung ermitteltem P-Influx von Maiswurzeln (10<sup>-14</sup> mol cm<sup>-1</sup> s<sup>-1</sup>)

Treatment	influx measured	root hairs omitted		root hairs included	
		influx calculated	calc. in % of measured	influx calculated	calc. in % of measured
P-0 NO <sub>3</sub>	0.56	0.10	18	0.26	47
P-0 NH <sub>4</sub>	1.03	0.10	10	0.28	28
P-200 NO <sub>3</sub>	3.47	2.18	63	2.86	82
P-200 NH <sub>4</sub>	6.53	2.29	35	5.30	81

root hair zone. The average root hair length was 0.47 mm. P concentrations at the root surface were decreased to very small values in case of P-0,  $\text{NO}_3^-$ :  $2.8 \times 10^{-12}$  mol  $\text{cm}^{-3}$ , and in P-0,  $\text{NH}_4^+$ :  $2.5 \times 10^{-12}$  mol  $\text{cm}^{-3}$ . This means that uptake caused almost the maximum possible P concentration gradient around the roots.

## Discussion

The results have shown that the P uptake of maize was markedly influenced by the N source the plants were supplied with. The increase in P uptake of  $\text{NH}_4\text{-N}$  compared to  $\text{NO}_3\text{-N}$  supplied plants cannot be attributed to an enhanced root growth as was reported by Riley and Barber (1971), because root/shoot ratio as a function of shoot P concentration was not different between the N forms (Fig. 2). More roots of the  $\text{NH}_4\text{-supplied}$  plants at low P supply were the result of more growth of root and shoot caused by higher P uptake. It is, therefore, concluded that the increased P uptake of  $\text{NH}_4\text{-N}$  supplied plants was brought about by an increased P influx per unit of root length rather than by changes in root growth.

Influx, for reasons of mass conservation, has to be equal to the P transport rate from soil to the root surface. This transport is mainly by diffusion and, therefore, the concentration gradient in soil solution is important. The calculation for the P-0 treatment based on the parameters of Table 3 showed (Fig. 4) that the P concentration at the root surface was decreased to a very low value. The concentration gradient and thus the possible transport rate to the root was almost maximum. Even so, the actual influx (Table 4) of  $\text{NO}_3\text{-N}$  supplied plants was 2 times and that of  $\text{NH}_4\text{-N}$  supplied plants 3.5 times higher than the calculated influx. The roots must, therefore, have increased the P concentration gradient in soil solution and thus the slope of the concentration profile (Fig. 4). This could not be achieved by further decreasing the concentration at the root surface, because it was already close to nil. A higher P uptake efficiency of the roots, as possibly caused by the presence of concomitantly absorbed  $\text{NH}_4\text{-}$  instead of  $\text{NO}_3\text{-ions}$  (Pilbeam and Kirkby, 1992), should, therefore, be ineffective. This is clearly evident from the comparison of calculated influx of  $\text{NH}_4\text{-N}$  or  $\text{NO}_3\text{-N}$  supplied plants with a high and a low  $I_{\text{max}}$  value, respectively (Tables 3 and 4 for low P supply). An increase of the concentration gradient could only be achieved by increasing the P concentration in soil solution, i.e. by increasing the solubility of soil P. It must be concluded that both, the  $\text{NO}_3\text{-}$  and the  $\text{NH}_4\text{-N}$  supplied plants were apparently able to do so but the effect was much larger for the latter.

An increased solubility of soil P is often attributed to changes in soil pH (Riley and Barber, 1971). In the soil used here, however, this effect was small as indicated by a relatively small effect of rhizosphere pH on P influx (Fig. 3). The higher P influx of  $\text{NH}_4\text{-N}$  supplied plants may be ascribed to the secretion of root exudates that solubilize

soil P or increase the microbial activity in the rhizosphere and thereby increase the contributions of organic or inorganic soil P to root P supply (Jungk et al., 1993; Seeling and Zasoski, 1993). Although these effects seem to be of great importance for plant P supply, they do not necessarily have to be measurable in the bulk soil. An increase in soil solution P concentration within the P depletion zone of roots (Fig. 4) would be sufficient to improve P transport to the root surface.

Possible mechanisms to raise P soil solution concentration are root excretions of organic acids. Application of citric acid to soils - including the oxisol used here - increased strongly the P concentration in the soil solution (Gerke, 1992). Gardener et al. (1983) demonstrated that the proteoid roots of P deficient *Lupinus albus* secreted large quantities of citrate. They suggested that citrate reacts in soil to form ferric-hydroxy-phosphate-polymers which diffuse to the root surface. Local acidification and the release of organic substances in the rhizosphere has been shown to be a reaction of plants on P deficiency (Hedley et al., 1982). Hoffland et al. (1989 a, b) detected local acidification and exudation of organic acids in the rhizosphere of rape roots as a response to P starvation. It could not be explained with changes in the nutrient uptake patterns along the root axis ( $\text{NO}_3^-$ , K, Ca). It was attributed to exudation of malate and citrate. Lipton et al. (1987) reported that citrate exudation from roots of P deficient alfalfa exceeded that of plants with adequate P supply by 182 %, while the release of malate was higher in the latter. Krzaczek et al. (1984) demonstrated that the release of organic acids of sterile maize roots was increased when maize was supplied with a nutrient solution containing  $\text{NH}_4\text{NO}_3$  instead of  $\text{NO}_3$  only. This indicates that  $\text{NH}_4$  as the N source may enhance the exudation of organic acids or other compounds that increase the release of P from the solid soil phase and thus support P acquisition.

Mycorrhizal fungi are known to collect P from soil when P availability is low and thus improve P supply of plants effectively (Tinker, 1975). Maize can serve as a host plant for VA mycorrhizae. Therefore, VAM could have contributed to the gap between measured and calculated P influx. However, the development of an effective ectomycelium was found to require about 4-6 weeks (Sutton, 1973) whereas our plants were grown for three weeks only. The enhancement of P uptake by  $\text{NH}_4\text{-}$  compared to  $\text{NO}_3\text{-N}$  nutrition could also hardly be explained by VAM. Furthermore, the difference between measured and calculated P influx at low P supply was also observed with *Beta vulgaris* (Hoffmann, 1993, p. 97), a member of the chenopodiaceae which does not host VAM. It is, therefore, concluded that the symbiosis of the plants with mycorrhizal fungi is unlikely to have appreciably contributed to the P supply of plants in this case.

The final conclusion derived from comparing results of measured P uptake and results of the model calculation is that P uptake from a well supplied soil could be explained

to more than 80 % (Table 4) by the mechanisms which constitute the basis of the model. These are transport from soil to roots by mass flow and diffusion and P uptake of roots according to Michaelis-Menten kinetics. The relatively good agreement of measured and calculated influx confirms earlier results (Barber, 1984; Föhse et al., 1991), showing that P uptake can be predicted by the model under these conditions. On the other hand, the gap between measured and calculated P influx suggests that under low P supply plants make use of additional mechanisms for P acquisition which are not part of the model. This is a type of information which can hardly be obtained by means other than model calculations. In addition, the model provides a quantitative estimate for such influences. They amount to 53 % in the plants supplied with NO<sub>3</sub>-N and 72 % in those supplied with NH<sub>4</sub>-N (Table 4, root hairs included). The role of root hairs in P acquisition can also be quantified (Table 4; see also Föhse et al., 1991). Furthermore, information on P depletion profiles of the soil solution near single roots as shown in Fig. 4 cannot be obtained easily by other methods.

Under this view, the model calculation used here appears to be a powerful tool in studying nutrient dynamics in the rhizosphere and in separating and quantifying the factors affecting it. The application of such a model to predict nutrient uptake of plants and fertilizer needs may be another aim. This aim, however, cannot generally be achieved yet with the model as it stands.

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