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The acquisition of soil nutrients by plants is a process that includes their transport through the soil solution to the root surface, entry into the plant and translocation to the sites of physiological need. If the nutrient is associated with the soil matrix it will have to be released into the soil solution by dissolution (for salts) or desorption (for adsorbed ions) prior to its transport to the root surface. Soil and plant properties will affect the overall process of nutrient acquisition, but the interaction between the soil and the plant is not straight forward. This can be recognized from the fact that plants grow similarly well and take up similar amounts of nutrients on soils differing widely in their properties including their nutrient content.

To analyze the soil-plant interaction I will describe the process of nutrient acquisition by the following equation

$$\frac{du}{dt} = Li_n \quad (1)$$

u is the amount of nutrient in the plant. The rate of uptake du/dt , ($\text{mol plant}^{-1} \text{s}^{-1}$) is given by the product of root length, L (cm plant^{-1}) and the influx, I_n ($\text{mol cm}^{-1} \text{s}^{-1}$). Instead of root length root surface, weight or volume may be used.

Equation (1) is a crucial one, because it shows that a factor which affects nutrient uptake may do so by changing the size of the root system, L , or the influx I_n or both.

Influx is the amount of nutrient crossing a unit of root per unit of time, it is a rate of transport and by mass conservation is equal to the transport of that nutrient from the soil to the root surface. The influx is a measure of the rate of transport to the root. Nutrient transport in soil is by mass flow and diffusion (Barber 1962). Under usual conditions of water uptake and root densities diffusion is much more efficient than mass flow and therefore the main transport mechanism at low but sufficient nutrient availability in soil. (Claassen, 1990).

The flux by diffusion, F_D ($\text{mol cm}^{-2} \text{s}^{-1}$) can be described by Fick's first law

$$F_D = -D_e \frac{dc}{dx} \quad (2)$$

D_e is the effective diffusion coefficient ($\text{cm}^2 \text{s}^{-1}$), C is the amount of diffusible nutrient, (mol cm^{-3} soil) usually the nutrient in soil solution plus the fraction of the solid phase in equilibrium with the liquid phase, and x is the distance to the root. The driving force for diffusion is the concentration gradient, dc/dx .

Since the diffusion takes place in the liquid phase of the soil D_e can be defined as follows:

$$D_e = D_L \theta f/b \quad (3)$$

Where D_e is the diffusion coefficient in water, θ the volumetric soil water content ($\text{cm}^3 \text{cm}^{-3}$), f the impedance or tortuosity factor and b the buffer power given by dc/dc_L . C_L is the soil solution concentration (mol cm^{-3} solution).
Now eq. (2) can be written

$$F_D = -D_e \theta f \frac{dc}{dx} \quad (4)$$

The flux to the root surface for a given ion will depend on the concentration gradient in soil solution, dc/dx and on the diffusion path characteristics given by the soil water content, θ , and the tortuosity of that path.

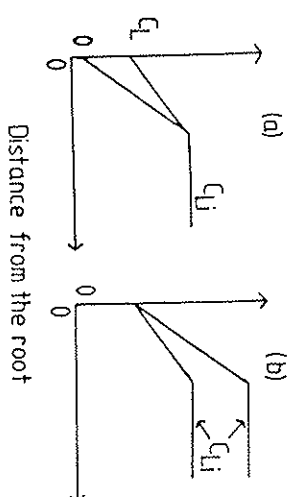


Fig.1 Schematic representation of concentration gradients in the rhizosphere. Plants can increase the concentration gradient by either stronger decrease of the concentration at the root surface (a), increase of the soil solution concentration, C_L , (b) or by both.

Equation (4) gives the factors affecting the flux by diffusion. Figure 1 shows how the plant may influence the concentration gradient. Furthermore it may be postulated, as I will show later, that plants also influence θ and f in the immediate vicinity of the root. After this introduction I will discuss some examples showing how the soil affects plant characteristics and how the plant affects soil characteristics and how these interactions finally affect the nutrient acquisition.

Interaction with soil physical factors

Soil water: It is generally accepted that soil water content affects the mobility of ions in soil through θ and f , eq. (3), (Barracough and Rinker, 1981) and would thereby influence the influx (eq. 1 and 4). Also, as the soil dries out root growth is reduced (Halmark et al., 1981). To which extent soil water content affects root growth and the influx and thereby nutrient uptake was investigated by Seiffert (1989) for K and by Köller (1989) for P. Both used soil filled pots with a perforated bottom so that the roots could grow through into a nutrient solution below without K or P. The soil was kept at a given moisture level

by watering through a plastic tubing with wicks put into the soil. Since water could be taken up also from the nutrient solution below, the plants had no water stress even if the soils were dry. This is a common situation in the field when the upper soil dries out. Different soil water content was imposed on the plants after the roots had reached the nutrient solution.

Figure 2 shows, for a soil low in K, that a decrease of the soil water content from 0.23 to 0.13 cm³ cm⁻³ reduced K uptake by about 70%. This was due in part to a reduced root growth but to a similar extent due to a decrease of the K influx caused by a reduced K mobility in soil (eq. (3) and (4)). At high K level in soil (data not shown) low water content had no effect on K uptake because the lower values of θ and f could be compensated by a larger concentration gradient (eq. (4) and Fig. 1). Simulation models based on the principles of eq. (2), (3) and (4) described the measured effects in a quantitative manner. Köllner (1989) found that P uptake by wheat was reduced from 1.6 to 1.3 mg P/plant when soil water content was reduced from 0.26 to 0.14 cm³ cm⁻³. This was, in contrast to the prior findings, only due to a reduced root growth (50 or 30 m root length per plant) while P influx stayed constant (see Fig. 3).

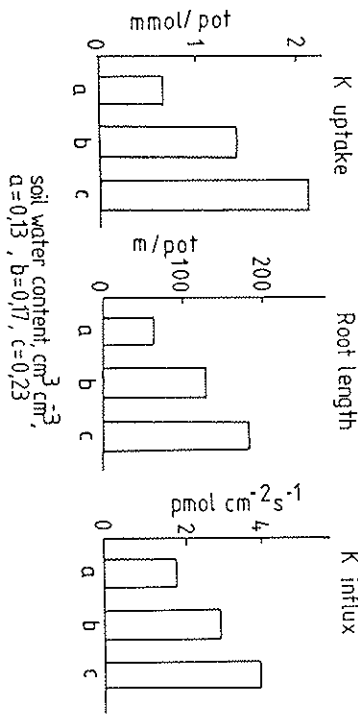


Fig. 2. Effect of soil water content on the K uptake of maize through its influence on root growth and K influx (Seiffert, 1989).

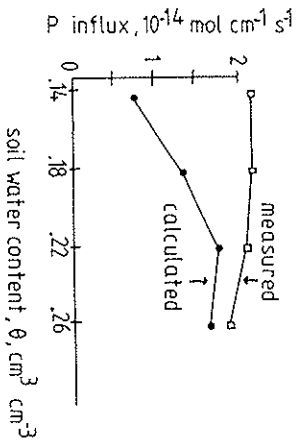


Fig. 3. Measured and with a simulation model calculated effect of soil water content on P influx of wheat on a P deficient soil ($C_{li} = 2.4 \mu\text{M}$). Calculations are based on the principles of eq. (2), (3) and (4) (Köllner, 1989).

This result was unexpected to us, but after all it may be not too surprising since it is not commonly heard that in dry years plant would show P deficiency. Kuchenbuch et al. (1987) found that in dry years root density in the upper soil decreased by a factor of 3 but the yield of maize on the unfertilized plot ($C_{li} = 1.6 \mu\text{M}$) was not affected. Therefore P influx must have been as high or even higher in dry than in wet years. Müller (1988) found that P influx of wheat during dry spells stayed constant or even increased somewhat. These results are unexplained to my knowledge. Because there is no doubt that soil water content does affect ion mobility in soil, and should therefore affect the influx in a similar way as shown by the calculations (Fig. 3). Plants must therefore be able to change the conditions in the rhizosphere which overcome the impairments of soil dryness. That this effect mainly works for P and not for K may be explained by the narrow depletion zone of P as compared to K, as shown in Fig. 4. I postulate that plants are able to keep a high volumetric water content even at low water potential in the bulk soil, and thereby P diffusion to the root is not affected by water content of the bulk soil as shown in Fig. 3. One would expect similar results for K, if plants mainly use nonexchangeable K which has a high buffer power and therefore a similarly low mobility as P.

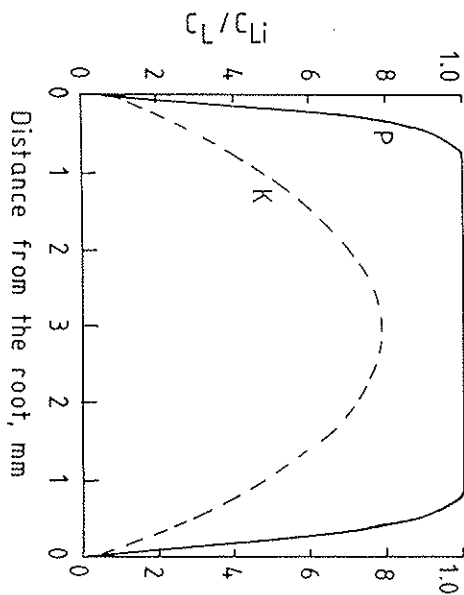


Fig. 4. Calculated concentration profiles of P and K in soil derived from loess with a water content of about 0.14 cm³ cm⁻³. For P and K respectively: $C_{li} = 2.4$ and $261 \mu\text{M}$, buffer power 337 and 7.2; Köllner (1989) and Seiffert (1989).

Soil compaction. Soil compaction may become a problem in modern agriculture due to the use of heavy machinery. Yield depression may be due to reduced root growth resulting in a reduced nutrient and water uptake or due to some physiological effects on the plant induced by high soil strength.

Kaselowky (1990) increased soil density by passing a heavy tractor over the soil. Prior to planting sugar beet the upper 10 cm were loosened again resulting in an average soil density of the plow layer of 1.65 g cm^{-3} as compared to 1.52 g cm^{-3} on the uncompacted plot. Maximum soil density of 1.73 g cm^{-3} was obtained between 10 and 15 cm. This experiment was carried out on a plot of low and a plot of high soil P. There was no difference in yield on both (Fig. 5), but the reduction was larger on the low P soil, suggesting that compacting the soil affected the P nutrition of the crop. This was not due to a reduced availability of soil P as evidenced by several soil parameters as P soil solution (Ca-Acetate-Lactate procedure). Therefore soil compaction affected the ability of the plant to acquire soil P.

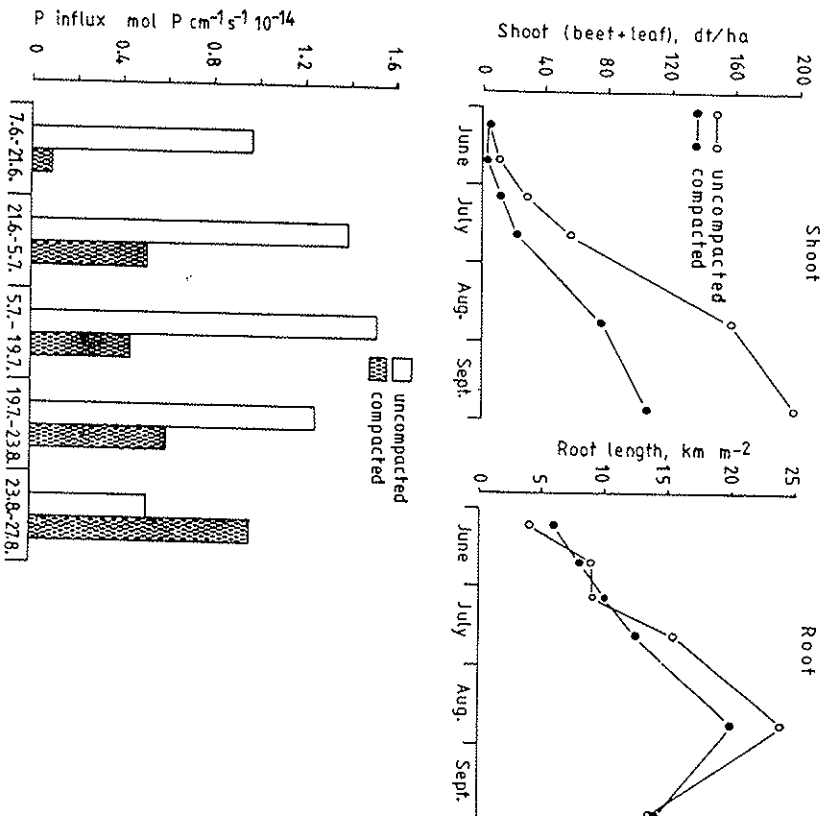


Fig. 5. Effect of soil compaction on shoot and root growth of sugar beet and P influx on a low P soil. P soil solution conc. $1.5 \mu\text{M}$ (Kaselowky, 1990).

Figure 5 shows that sugar beet growth was reduced by soil compaction, the effect being strongest early in the season. Total root growth was less affected, and early in the season there was even no effect. The higher root length on the uncompacted soil in July and August was due to an increased root growth in the 10 - 30 cm layer. The effect of soil compaction on P influx was dramatic, it was reduced to 11 % of that on the uncompacted soil. Since the parameters of P availability of eq. (2), (3) and (4) were almost unaffected (see above) compaction of the soil must have influenced the physiological ability of the root to extract soil P. The conclusion from this experiment is that soil compaction or soil strength not only affects root growth (root length) but also, and even to a greater extent, root physiological properties. Based on measured soil parameters (Cl_i , b , D_e , θ , f) and plant parameters (root length and root uptake characteristics) P uptake was calculated with a simulation model based on the principles of eq. (2), (3) and (4). These results were compared with measured uptake (Fig. 6).

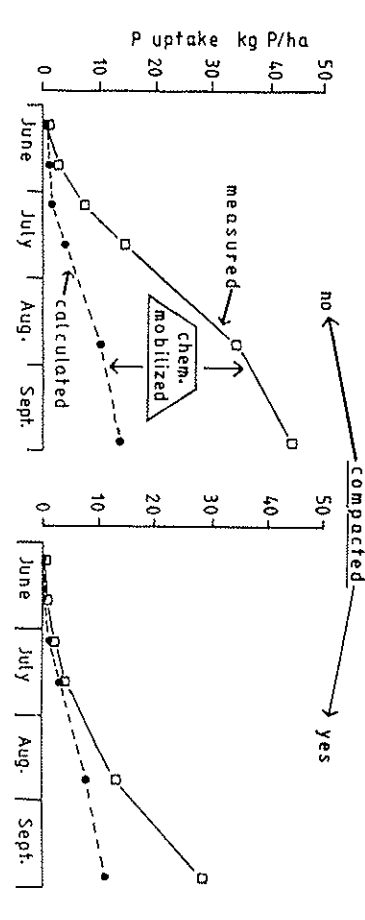


Fig. 6. Effect of soil compaction on the capability of sugar beet to mobilize P chemically. The P taken up in excess of that calculated is assumed to have been mobilized chemically (Kaselowky, 1990)

It can be seen that sugar beet took up more P as calculated by the model. This difference would be due to processes or factors not accounted for in the model. It is assumed that this process is chemical mobilisation of P by exudation of substances by the root that increase the solubility of soil P, like shown in Fig. 1(b). Since this process occurs just in the narrow zone of P depletion (see Fig. 4) it might not be detected by analyzing the bulk soil, as was done in this experiment. Chemical P mobilisation was much larger on the uncompacted than compacted soil. While on the uncompacted soil chemical mobilisation started already in June, it was absent on the compacted plot until mid of July. Higher soil strength apparently affects root physiology in a way that exudation of mobilizing substances is inhibited. Oussible et al. (1992), using a similar technic as above, found a decrease of shoot but almost no effect on total root growth of

wheat on subsurface compacted soils. There was a decrease of root growth in the compacted layer of 20 % in one year and 36 % in the other while effect on yield was the inverse, i.e. 25 % and 13 %. It therefore seems that soil strength influences shoot growth more by physiological effects on the plant rather than on its effect on the size of the root system.

Interaction with chemical soil factors

Figure 1b shows that transport of nutrients to the root and thereby the influx can be enhanced by an increased soil solution concentration. This could be achieved by fertilization, of course, or by changing the solubility of sparingly soluble salts or by an increased desorption of adsorbed ions. The latter (higher solubility or desorption) if induced by root activity is usually called chemical mobilisation of nutrients. In this chapter I will only consider the influence of the root on chemical properties of the soil and not the inverse case.

Changes of pH in the rhizosphere. Soil pH has a broad effect on the solubility of nutrients and thereby on the concentration gradient between the soil and the root (see Fig. 1b). Plants can influence the pH in the rhizosphere depending on the balance of cation and anion uptake or by the exudation of organic acids. A surplus of cation over anion uptake and therefore an acidification occurs when plants absorb N mainly as NH_4 or when legumes fix N_2 symbiotically. Some surplus of anion uptake may occur when N is absorbed as NO_3 .

It is generally accepted that a decrease in soil pH increases the solubility of micronutrients with the exception of Mo. The effect on P will depend on its binding in the soil, whether as a salt or adsorbed to the solid phase. The P fraction extracted with a base (usually NaOH) called Fe and Al phosphate ((Fe-Al)-P) actually seems to be adsorbed to Fe and Al hydroxides since this fraction is isotopically exchangeable while the acid extractable P is designated as Ca phosphate (Ca-P) seems to be a salt which is only slightly accessible to isotopic exchange (Machold, 1962). Figure 7 shows that rape, which did not change the pH in the rhizosphere, only depleted the so called (Fe-Al)-P, i.e. adsorbed P, and only a decrease of the rhizosphere pH by mustard caused some depletion of Ca-P. It therefore seems that plants feed mainly on the adsorbed P in soil which is in accordance with Machold (1962), and Ca-P can only be utilized if the plant decreases the pH in the rhizosphere. The latter is the case when legumes fix N_2 , enabling soybean for example to use rock phosphate only if no NO_3 -N is supplied (Aguilar et al., 1981). A pH decrease is also observed when plants feed on NH_4 -N (Gahomnie et al., 1992) or when organic acids are exuded, often as a response to P deficiency in rape (Hoffland et al., 1989) or in white lupine (Dinkelaker et al., 1989).

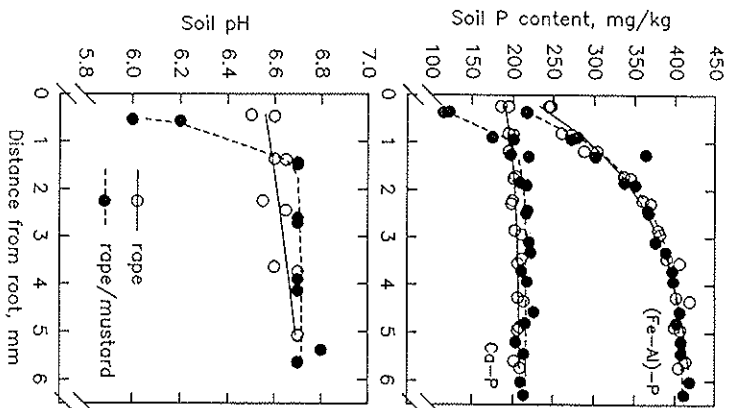


Fig. 7. Depletion of different soil P fractions in the rhizosphere of rape or rape plus black mustard and its relation to the pH (Wedemeier, 1990)

Root exudates. Changes in soil pH as described above, have a broad and general effect. But plants have developed much more specific and sophisticated mechanisms to mobilize nutrients. The solubility of Fe in well aerated soils is so low that plants would be unable to obtain sufficient of it except they increased the Fe concentration in soil solution at the soil root interface. The mechanisms by which plants mobilize Fe in soil have been investigated extensively and described by Römheld et al. (1986). The increase of Fe solution concentration is achieved depending on plant species, either by decreasing soil pH and increasing the reducing capacity or by the secretion of Fe chelators (called phytosiderophores) that complex Fe specifically increasing Fe concentration in soil solution. This Fe chelate is then transported to the root and absorbed without splitting the Fe from the chelator. Phosphorus concentration is not as low as that of Fe but in many cases chemical mobilisation is required to explain the amount of P

taken up (see Fig. 6). The mechanisms may be by pH changes, as shown before, or secretion of specific substances that are able to increase the P concentration in soil solution. Ae et al., 1990 found that the ability of pigeon pea to thrive on a low P Alfisol was associated with the secretion of piscidic acid that solubilized P from Fe phosphate. The secretion of citrate by white lupin has been investigated in more detail. Citrate may increase P solution concentration by ligand exchange on the sites of P sorption. When phosphated ferric hydroxide (Gardner et al., 1983) or soils (Gerke, 1992) were shaken with citrate P concentration increased drastically. However, the increased P in solution was associated to large molecules together with Fe and Al. The zone of citrate secretion (proteoid roots) also shows an increased reducing capacity. From these findings Gardner (1983) proposed the model shown in Fig. 8.

Citrate secreted by the root picks up Fe and then forms a soluble polymer with phosphate, increasing P solution concentration and thereby its rate of transport to the root (see Fig. 1). The root reduces the Fe^{3+} of the polymer to Fe^{2+} and P is released which then can be taken up.

Therefore the mechanism of chemical mobilisation has to show the substance released, explain how the concentration in solution is increased, account for the higher transport rate to the root and at the same time explain how the nutrient, if chelated or associated to large molecules, is taken up by the plant.

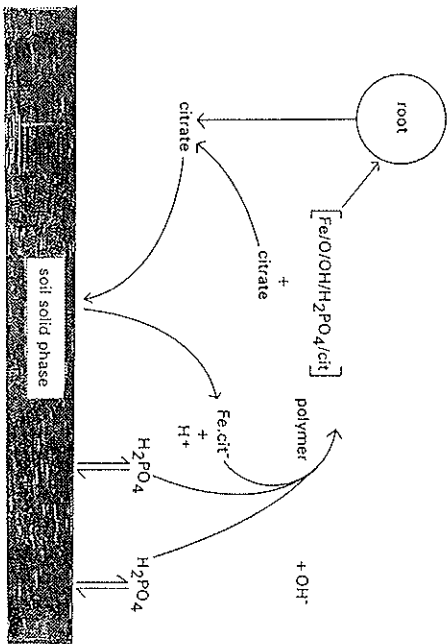


Fig. 8. Proposed reaction sequence between citrate, iron and phosphate in soil (Gardner et al., 1983).

Conclusions

Nutrient acquisition by plants is the product of root length (cm mol^{-1} and influx ($mol\ cm^{-1}s^{-1}$)). Analysing the effect of any factor the influence on both of them has to be evaluated. Soil physical factors like water content and soil density affected both, root length and influx but not always as expected. Soil water content did affect K but not P influx. Soil density had a larger effect on the influx by reducing the physiological capability of the root than on root growth. The root affects the pH of the rhizosphere or may secrete substances that increase the solubility of nutrients. The resulting larger concentration gradient between the soil and the root causes a higher transport rate to the root and thereby higher influx. Plants have developed sophisticated mechanisms of chemical mobilisation of nutrients in soil.

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