Interpretive Summary of Part 2:
Extraction of Soil Phosphorus by Plant Roots

N. Claassen[1]

Introduction

The first part of this book deals with phosphorus (P) in soil and its chemical behavior in relation to its availability to plants. This second part concentrates on plant factors, specifically, on the root and its role in P acquisition from soil.

The System: Its Components and Functioning

The system we are concerned with consists of the root surrounded by soil. The supply of P to the root depends on soil properties such as P content, chemical form of P compounds, and the mobility of this P in soil. These properties constitute the P availability of a soil. The amount of P a plant can extract from this available P depends on its root length and on morphological and physiological properties of the root. These plant properties comprise the acquisition capacity of the plant. In the following I will describe the components of the system and its functioning, including the interaction among the components.

The Root

In the process of P transfer from the soil to the plant, the root functions as the absorbing organ, as a sink. The root may also enhance this process by changing the chemical environment in the rhizosphere and thereby making P more available.

The properties of the root related to the absorption of P were treated in depth and detail by Clarkson and Grignon (1991). Reviewing the literature, they concluded that P uptake or transfer from the outside of the plasma membrane into the cell is facilitated by a secondary active transport system. The biochemical mechanism for this transport system is not known at

the molecular level. Clarkson and Grignon have also described several properties of the transport system and how it reacts to proton concentration.

Two factors of the transport system seem of practical interest for the nutrition of crops, i.e., its very low K_m (Michaelis constant) value and the regulation of its uptake capacity according to the P supply in the external solution. This is shown in Figure 1 for soybean grown in flowing nutrient solution of various P concentrations. While the K_m value was similar for all treatments (1.0-1.7 μmol P L^{-1}) the maximum influx

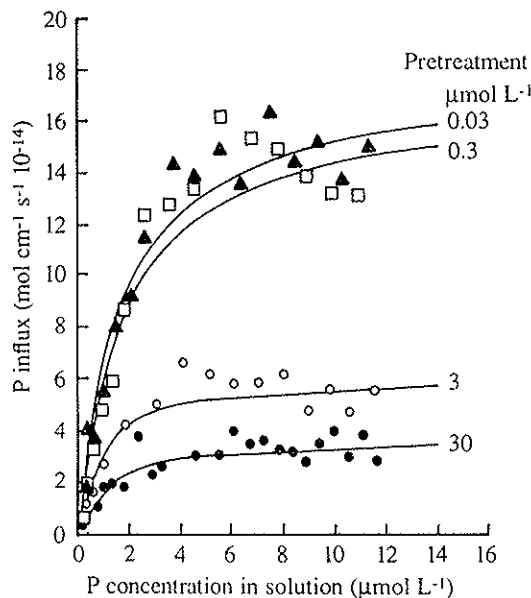

Figure 1. Phosphorus-uptake isotherms for soybean grown in flowing nutrient solution of various P concentrations (pretreatment) (Jungk et al. 1990).

(I_{max}) increased from 3.7×10^{-14} to 17.6×10^{-14} mol cm^{-1} s^{-1} when the P concentration during pretreatment was reduced from 30 to 0.03 μmol L^{-1}. The K_m value observed in this experiment is somewhat higher than that reported by Clarkson and Grignon for the transporter itself. This is because the experiment was conducted with intact roots, where the plasma membrane is separated from the nutrient solution by the cell wall.

The increased I_{max} at low external P concentration is probably due to an increased synthesis of P transporters in the plasma membrane. This is an adaptation that enables plants to obtain enough P even at very low concentrations.

The properties of the transporter described above lead Clarkson and Grignon to the very important conclusion that "this flexibility ensures that plant growth is rarely limited by the ability of roots to absorb P_i (inorganic P). It is much more usual for the supply of P_i to the absorbing mechanism to be limiting uptake." The P nutrition of crops will therefore mainly depend on the capacity of the soil to supply P to the root surface. This aspect will be treated later.

The root not only acts as a sink for P but may also change the chemical and biochemical environment of the rhizosphere (the soil surrounding the root). It is well known that roots change the pH of the soil, secrete reducing or chelating substances, and increase the activity of soil microorganisms. By these processes, roots affect the availability of soil nutrients.

Takagi (1991) showed the elaborate system that grasses have developed to acquire iron (Fe) from sparingly soluble compounds. With Fe deficiency, the roots of grasses enhance the release of ferric-specific ligands, called phytosiderophores, which have been identified as amino acids analogous to mugineic acid. These phytosiderophores, after being released, have the function of forming very stable Fe(III) complexes which are then carried back into root cells via a matching transport system.

Chemical mobilization of P has been postulated many times. This process may be of great significance for the P nutrition of crops, as Figure 2 illustrates. There, P uptake of sugarbeet was measured in the field, on the one hand, and calculated by a model that did not include chemical mobilization by the root, on the other. Calculations were performed with a model based on the principles discussed by Amijee et al. (1991), but which included root hairs. The difference between measured and calculated P uptake may therefore be attributed to chemical mobilization of P. As can be seen at low soil-solution concentrations of P, up to 75% of P uptake may be chemically mo-
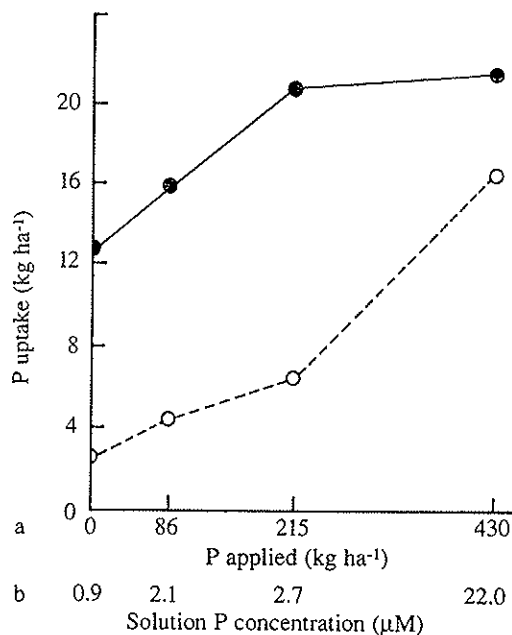

Figure 2. Phosphate uptake by sugarbeet in July at different (a) P fertilizer rates and (b) solution concentrations. ● = measured, ○ = calculated by a simulation model including root hairs (Claassen 1990).

bilized by the roots of sugarbeet.

The significance of P mobilization for the P nutrition of pigeonpea on an Alfisol was also shown by ICRISAT (1989). While sorghum showed almost no growth and chickpea only 50% of its maximum yield on a nonfertilized soil, pigeonpea attained full yield on the same soil. This high yield potential of pigeonpea was attributed to its capability to solubilize Fe-P, which is the main P fraction of the Alfisol used.

Several mechanisms have been proposed for P mobilization by plant roots, but the exact functioning, as shown before for Fe, is not yet known.

Phosphorus mobilization has often been attributed to root-induced pH changes in the rhizosphere, as shown in Figure 3 (Gahoonia 1987). The observed decrease of pH in the rhizosphere due to ammonium-N (NH_4-N) application, even so little as 10 mg N 100 g^{-1} soil, is associated with a large depletion of P at the root surface. When, in another experiment, the soil was acidified artificially with H_2SO_4, P depletion at the root surface was also increased, but to a much smaller extent, indicating that factors other than pH also influenced P mobilization of NH_4-fed plants.
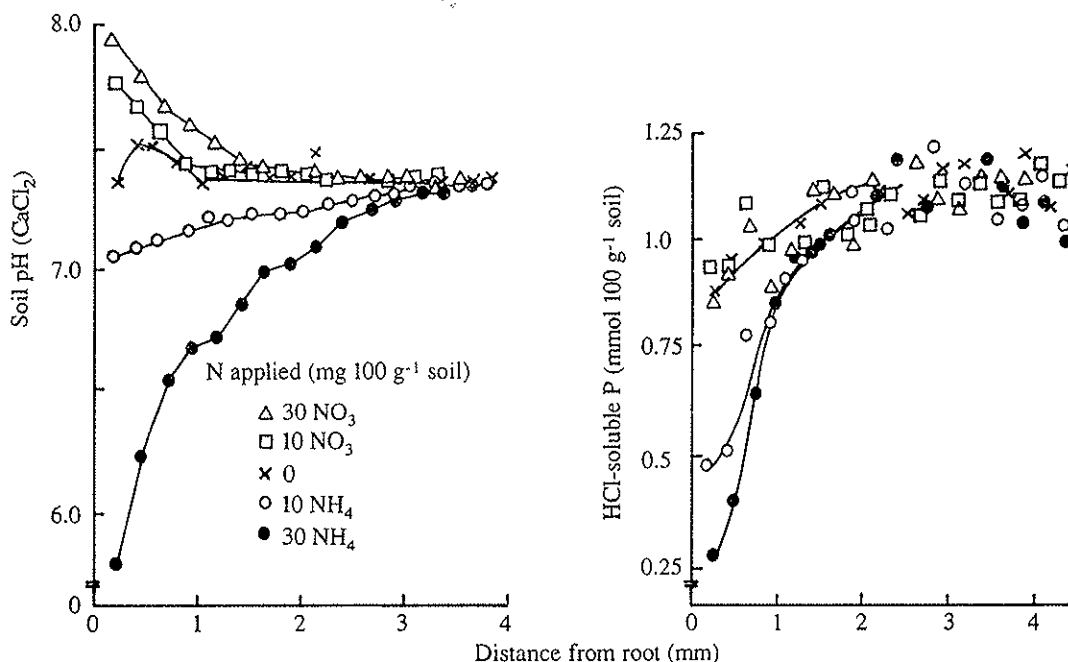
Figure 3. Soil pH changes and P depletion in the rhizosphere of 10-day-old ryegrass as influenced by ammonium-N (NH_4) and nitrate-N (NO_3) nutrition (silt loam soil formed from loess) (Gahoonia 1987).

These findings are in accordance with those of Gardner et al. (1983), who concluded that P mobilization of white lupin is not so much based on the decrease in rhizosphere pH as caused by the secretion of citrate. They proposed that citrate would form a polymer with Fe and P, increasing P concentration in soil solution and thereby its transport to the root.

Equally interesting are the findings of Ae et al. (1991). They found that pigeonpea grows better than sorghum, soybean, or maize on an Alfisol where P is mainly in the form of Fe-P. This difference did not show up on a Vertisol containing a much greater proportion of Ca-P. When grown in sand culture with $FePO_4$ or CaH_2PO_4 as a P source, pigeonpea utilized both forms of P equally efficiently, while the other species hardly grew with $FePO_4$. After a detailed and elaborate study of root exudates, Ae and his coworkers were able to identify piscidic acid as the substance responsible for the mobilization of Fe-P by pigeonpea. When piscidic acid is added to sparingly soluble $FePO_4$ it increases P solution concentration.

Research is needed to assess the mode of action of piscidic acid in the soil/root system: its release by

pigeonpea roots and factors affecting it, how P solubilized by piscidic acid is utilized by the plant, whether it is released at the surface of the plasma membrane before uptake or is taken up as a complex, as was shown for Fe bound by phytosiderophores (Takagi 1991).

The P-uptake capacity of a root system depends not only on physiological properties of the root, as previously discussed, but also on morphological properties, such as root radius and root hairs, and on the length of the root system. Another distinct feature related to P uptake by crops is the symbiosis with mycorrhizal fungi, which is treated in Part 3.

The P nutrition of a crop depends on the capabilities of its root system. This obvious statement emphasizes, however, the necessity of quantifying those root properties, including the root-growth pattern, in order to be able to understand the P nutrition of a crop.

The Soil

Clarkson and Grignon reached the conclusion that

even very low P concentrations hardly limit growth, because plants adjust their uptake system to the P concentration. Therefore, soil-grown plants will show P deficiency because of an insufficient P supply to the root surface rather than because of a low concentration in soil solution itself.

The total amount of P in soils is usually large. Even those soils described by Ae et al., which were deficient in P for plant growth, contained 122 and 153 mg P kg^{-1}; i.e., about 400 to 600 kg P ha^{-1} in the plow layer. The low availability of this P is because of the low P concentration in soil solution, which limits P transport to the root surface.

For P transport in soil, diffusion rather than mass flow is the mechanism of major significance. The flux by diffusion, F, is given by

$$F = -D \, dC/dx \qquad (1)$$

where D is the diffusion coefficient in soil and dC/dx the concentration gradient (see also Amijee et al.). Since P movement in soil is only in the liquid phase, we can write

$$D = D_l \, \theta \, f_l (dC_l/dC) \qquad (2)$$

where D_l is the diffusion coefficient of P in water; θ is the volumetric soil water content, which determines the cross-sectional area through which P can diffuse; f_l is the impedance or tortuosity factor, which, for a given soil, increases with θ; C_l is the P concentration in soil solution; C is the P concentration in soil participating in the diffusion process; dC_l/dC is the slope of the desorption curve, its inverse being the buffer power, b.

Two important consequences follow from the fact that P only diffuses in the liquid phase. First, the concentration gradient driving the flux by diffusion is that in the soil solution; a low soil solution concentration means a small concentration gradient. The transport to the root, and thereby P uptake, can only be increased by increasing P concentration in soil solution. This, as was already seen, happens when pigeonpea secretes piscidic acid. Second, soil water content has a dominant effect on D and therefore on the transport to the root (Equations 1 and 2). This is of major significance for the semi-arid tropics, where the soil water regime may vary from waterlogging to permanent wilting point in the course of a growing season.

Other chemical aspects of P in soil that are relevant to its availability to plants were, in part, treated together with P mobilization by plants, but mainly in the papers in Part 1.

Soil × Plant Interactions

The uptake of P by the plant is the result of the interaction of the plant with the soil. Some of these processes were treated in describing chemical mobilization of P by the plant. On the other hand, processes involved in P uptake by the root from soil solution and P transport in soil were treated separately. In reality, however, they proceed at the same time; furthermore, they influence each other.

One way to describe and study this complex system is by mathematical simulation models. To do this, the processes involved and the factors affecting them must be known, and a mathematical description of them given, as shown in Equations 1 and 2 and the Michaelis-Menten formalism for ion influx into roots (see also Amijee et al. 1991, in this volume).

Amijee et al. presented a thorough review of the models on nutrient uptake, starting with the prototypes from the 1960s. They showed the structure of the models, the assumptions and simplifications made as well as their limitations. Most models consider the root only as a sink; neither chemical mobilization through root exudates nor root hairs are normally included. In some cases, results calculated with those models agreed with observed data. In other cases, mainly at low P levels in soil, observed P uptake was higher than that calculated. This suggests that root hairs or chemical mobilization are operative. Thus it is possible to use these models to assess the significance of root hairs or P mobilization by roots.

Simulation models are also useful for assessing the significance of soil and plant parameters by means of sensitivity analysis. They show that, of the soil parameters, soil-solution P concentration is the one that most influences P uptake by a crop, followed by soil water content, θ. Of the plant parameters, root length is of major importance, but the parameters of Michaelis-Menten kinetics may also be significant, especially if P uptake is by root hairs or mycorrhizal hyphae. Because of their small radius, soil-solution concentration is not much decreased at the absorbing surface of hyphae (Barber 1984; Claassen 1989).

Another soil × plant interaction is that of soil water content and P uptake. This interaction is complex. The effect of soil water on P transport in soil has already been treated. But, on the one hand, low soil water content reduces root growth (Pearson 1966) and, on the other, promotes root-hair growth (Mackay and Barber 1987) and root-exudate production (Nam-

biar 1976). The outcome of these opposing effects is difficult to predict. More detailed investigations are therefore required on this aspect, particularly for the semi-arid tropics, where soil water content may vary considerably during the growth period.

Research Requirements

An aim of research at ICRISAT is to improve management practices through a better knowledge of the dynamic soil-plant system; i.e., of its components and their interactions. Knowing the way a system functions enables the formulation of management practices that will help improve the P nutrition of plants.

Necessary Measurements and Procedures

To understand the processes and factors involved in P uptake from soil, some of the measurements should be taken repeatedly during the crop growing season:

- root and shoot development;

- P uptake and P influx into the root (mol P cm^{-1} root s^{-1});

- root exudates;

- root properties, such as root length, root radius, and root hairs;

- soil parameters during the growing season, such as soil water content, soil-solution P concentration, and labile P.

Furthermore, models should be used to test whether the system is understood and/or to make predictions on the behavior of the system. The models that could be used have been presented by Amijee et al., but less complex models may also have a role. For example, to test whether root competition is likely, the extension of the P-depletion zone, Δr, can be estimated by

$$\Delta r = \sqrt{2Dt} \qquad (3)$$

where D is the diffusion coefficient of P in soil and t is time of diffusion, which may be equated to time of uptake of a root segment.

Topics of Special Interest

Some of the topics that need further investigation have already been referred to in the description of the soil-plant system. They will be restated here together with other topics.

Soil moisture is a dominant growth factor in the semi-arid tropics; therefore, research should be done on:

Effects of soil water and sequential soil drying on P uptake in different soil types. Important and necessary measurements should be root-length development and P influx (mol cm^{-1} s^{-1}), among others.

The mechanism of chemical P mobilization. Since chemical mobilization of P by crops, especially by pigeonpea, is a vital process in P acquisition, further research is needed on the mechanism of chemical P mobilization. The utilization of soil P by plants depends on its chemical nature. For example, pigeonpea mobilizes Fe-P, which is a useful way to obtain P from an Alfisol. Vertisols have more Ca-P than Alfisols, but still have relatively large amounts of Fe-P. The extent to which this Fe-P is accessed by pigeonpea is not clear. Therefore, more research is needed on chemical characterization of soil P and relative availability of the different P components to crop species. Can other species, growing together or in sequence with pigeonpea profit from the P mobilized by pigeonpea? If so, what are the mechanisms?

Methods of P application and its timing in a crop rotation. Pigeonpea has been shown to utilize FePO$_4$ very efficiently. However, although iron phosphate ore reserves are relatively large (McClellan and Gremillion 1980), they have not been used as a fertilizer source. Therefore investigations are needed into the possibility of using FePO$_4$ as a P fertilizer for field-grown pigeonpea. In the same project, it should be investigated whether the P obtained by pigeonpea from FePO$_4$ and returned to the soil by crop residues is then available to other crops.

The proposed topics are by no means exhaustive and should be looked at as a part of a future research approach.

References

Ae, N., Arihara, J., and Okada, K. 1991. Phosphorus uptake mechanisms of pigeonpea grown in Alfisols and Vertisols. (In this volume.)

Amijee, F., Barraclough, P.B., and Tinker, P.B. 1991. Modeling phosphorus uptake and utilization by plants. (In this volume.)

Barber, S.A. 1984. Soil nutrient bioavailability. New York, NY, USA: John Wiley.

Claassen, N. 1989. Die Aufnahme von Nährstoffen aus dem Boden durch die höhere Pflanze als Ergebnis von Verfügbarkeit und Aneignungsvermogen. Habilitationsschrift, Universitat Göttingen. Göttingen, Federal Republic of Germany: Severin Verlag.

Claassen, N. 1990. Fundamentals of soil-plant interactions as derived from nutrient diffusion in soil, uptake kinetics and morphology of roots. Pages 118-123 in Transactions, 14th International Congress of Soil Science, 12-18 Aug 1990, Kyoto, Japan. Vol. 2, Commission II.

Clarkson, D.T., and Grignon, C. 1991. The phosphate transport system and its regulation in roots. (In this volume.)

Gahoonia, T.S. 1987. The influence of plant induced pH change in the rhizosphere on the availability of soil phosphate. Ph.D. thesis, University of Göttingen, Göttingen, Federal Republic of Germany. 93 pp.

Gardner, W.K., Barber, S.A., and Parbery, D.G. 1983. The acquisition of phosphorus by Lupinus albus L. III. The probable mechanism by which phosphorus movement in the soil/root interface is enhanced. Plant and Soil 70:107-124.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1989. Pages 97-98 in ICRISAT Annual report 1988. Patancheru, A.P. 502 324, India: ICRISAT.

Jungk, A., Asher, C.J., Edwards. D.G., and Meyer, D. 1990. Influence of phosphate status on phosphate uptake kinetics of maize and soybean. Plant and Soil 124:175-182.

Mackay, A.D., and Barber, S.A. 1987. Effect of cyclic wetting and drying of a soil on root hair growth of maize roots. Plant and Soil 104:291-293.

McClellan, G.H., and Gremillion, L.R. 1980. Evaluation of phosphatic raw materials. Pages 43-80 in The role of phosphorus in agriculture (Khasawneh, F.E., Sample, E.C., and Kamprath, E.J., eds.). Madison, WI, USA: American Society of Agronomy.

Nambiar, E.K.S. 1976. The uptake of zinc-65 by oats in relation to soil water content and root growth. Australian Journal of Soil Research 14:67-74.

Pearson, R.W. 1966. Soil environment and root development. Pages 95-126 in Plant environment and efficient water use (Pierre, W.H., Kirkham, D., Pesek, J., and Shaw, R., eds.). Madison, WI, USA: American Society of Agronomy and Soil Science Society of America.

Takagi, S. 1991. Mugineic acids as examples of root exudates which play an important role in nutrient uptake by plant roots. (In this volume.)

Part 3

Improving the Phosphorus Nutrition
of Grain Legumes
in the Semi-Arid Tropics