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Phosphorus; elusive but essential

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Abstract

Phosphorus is an essential plant nutrient that is considered, despite its abundance in the earths crust, as one of the least available nutrients to plants. Plants can only take up mineral nutrients from the soil solution and phosphorus is taken up in the form of phosphate. Because the soil solution is constantly mined for nutrients it is important that the mineral contents are steadily replenished, this is done by mineralization of organic compounds that become labile and are then exchanged with the soil solution. In the mineralization process bacteria and fungi play a key role. Despite this mineral cycling that happens in the soil plants have developed a few more ‘tricks’ to maximize nutrient uptake. They can have a symbiotic exchange with mycorrhizal fungi and they can form specialized root structures, named cluster roots, which enhance surface area and the influence of the exuded compounds in these cluster roots. Because P_i is such a scarce nutrient in the soil solution farmers apply it directly in the form of mineral fertilizers. However a large part of the applied fertilizers becomes unavailable rather quickly and thus continuous over-application is necessary to maintain steady crop production. This results in a breaking of the P-cycle where P eventually ends up in surface waters and can hardly be reclaimed for application on agricultural land. Because this can obviously not continue indefinitely a lot of research is being done on alternative ways of soil fertility management. Although results point in the direction of the application of more organic alternatives such as farmyard manure and compost, it should be considered that the current crop varieties might not be adapted to a sudden change of soil management. This poses farmers and researchers both with a tremendous challenge but also with previously unexplored possibilities. It should be questioned how can plants maximize the uptake of phosphorus and how can good soil management maximize and sustain phosphorus availability?

Content

Introduction

Although phosphorus is quite abundant in the earths crust it is only partially present in plant available form, making it the second most frequent limiting plant nutrient. Phosphorus is an essential macro-nutrient for plants, in a developed plant it is about 0.2% of the dry-weight of the plant (Taiz and Zeiger, 2002), and it is essential for plant growth and development. Mainly because its pivotal role in all energy requiring reactions, besides this it is also incorporated in phospholipids in membranes and also in nucleic acids which carry the genetic material of all living organisms.

Phosphorus is unlike for example nitrate not a global element, which means that in its cycle it is never very mobile, this makes the cycling back into the soil all the more important because once taken up from the soil it will not be replaced unless the organic matter is locally decomposed again. This necessity is at the heart of the current problem that makes Phosphorus essential and interesting to study.

Through thorough understanding of both the mechanisms developed in plants to enhance P_i (inorganic phosphate) uptake and the processes that take place in soils that influence P_i availability we can gear our soil management practices to the needs of any given particular soil-plant system to enhance efficiency, productivity and ultimately reach absolute sustainability. The questions that must be answered to come to a proper understanding of both the plant and the soil factors of the equation are the questions that will be central to this paper. *How can plants maximize the uptake of Phosphorus; and how can proper soil management practices lead to maximized and sustained* *availability of phosphorus?* To answer these questions in a logical and organized way the plant and its needs are central in the discussion and thus considered first. Soil properties that influence P_i availability to these plants are discussed secondly and also in this chapter soil life and its role in the nutrient cycle are included. Finally when the consensus on what plants need is established, a chapter on the manner of how agriculturalists can provide the ideal conditions to crop plants is provided.

Phosphorus in plants

Usage/incorporation of P

Phosphorus is used in all energy demanding reactions, it is incorporated in phospholipids for membranes and nucleic acids (Stevenson and Cole, 1999; Schachtmann et al., 1998). P deficiencies in plants lead therefore to stunted growth and delayed maturation, also older leaves can fall off and remaining leaves change to a very dark green colour (Taiz and Zeiger, 2002)

Uptake of P

Phosphorus is after Nitrogen the second most frequently limiting macronutrient in plants (Schachtman et al., 1998). Plants acquire phosphorus in the form of phosphate anions - often denoted simply as P_i where i stands for inorganic - from the soil solution through active transport. The orthophosphate - $H_2PO_4^-$ - form is generally the preferred form for transporters (Ragathoma and Karthikeyan, 2004). Which is also the most abundant at moderate soil acidity as can be seen in Fig.1.

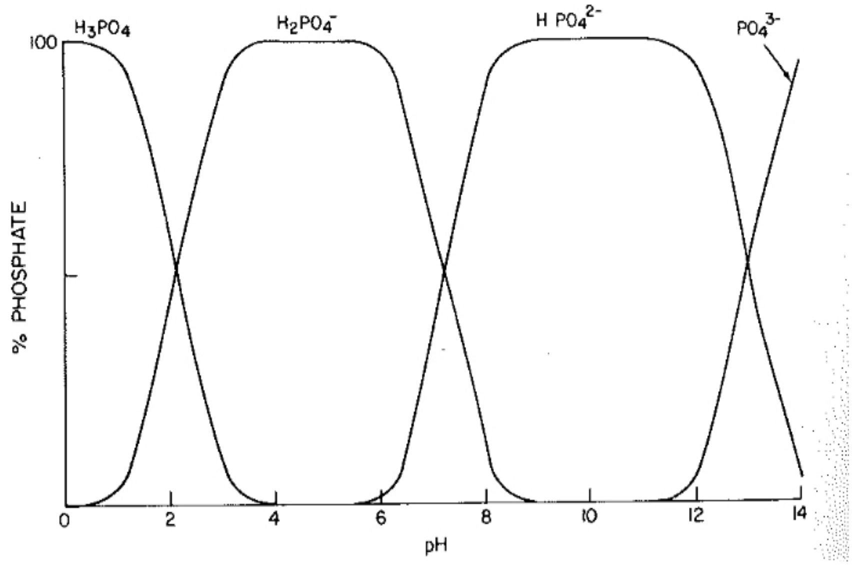

Fig 1. pH distribution of the phosphate-series (Bohn et. al., 2001).

Ions such as P_i can diffuse freely into the apoplasm, the plasmalemma however prevents further diffusion into the symplasm, this and the steep electrochemical gradient demands active transport for P_i uptake. (Smith, 2000; Raghothama, 2000; Schachtmann, 1998) The movement of P_i *across* the plasmodesmata is the critical step in the uptake process and requires energy-driven transport. Active transport of $H_2PO_4^-$ occurs via co-transport with a H^+- cation, this in turn is dependent on the activity of a H^+-ATPase which pumps H^+-ions out of the symplasm (Smith, 2002; Fig. 2)

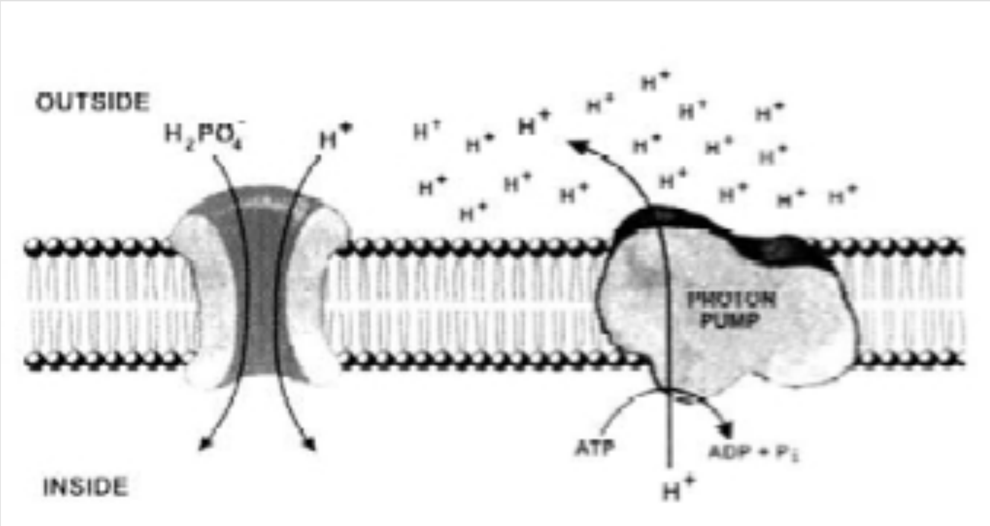

Fig. 2. $H_2PO_4^-$ uptake by use of H^+ gradient.

For transport multiple transporters have been identified, namely high affinity and low affinity transporters, the former only being activated when P-deficiency is detected in the soil solution (Ragathoma and Karthikeyan, 2004). The difference between high and low affinity transporters should not be thought of in terms of an absolute P_i concentration barrier where one system is shut off completely and another takes over. The low affinity transporters are active continuously while the high-affinity transporters are only activated at lower P_i content of the soil solution (Smith, 2000). Although a lot of research has been conducted in this area, complete clarity has yet to be achieved especially concerning the regulatory process that activates the high-affinity system.

When plants take up P_i from the soil solution, a P-depletion zone around the roots is formed. Plants have 'developed' several strategies to enhance the amount of soil that is being explored for P_i or the amount of P_i that is available for uptake in the rhizosphere.

Mycorrhizae

Mycorrhiza literally meaning in latin: *mykos*; fungus and *riza*; root → 'fungusroot' is an ancient symbiotic association wherein the fungus explores extra soil for the plant, especially obtaining P_i in exchange for sugars made in the plants photosynthesis (Miyasaki et al., 2007; Bolan et al., 1991; Foehse et al., 1988). Within the mycorrhizae a distinction can be made between endo- and ectomycorrhizae, the difference being how the fungus colonizes the root. The most common form in crop plants are the arbuscular mycorrhizae (AM), which are a sort of endomycorrhizae, this means that the fungus colonizes the root cortex both inter- and intracellulary (Barea et al., 2008).

Establishing a symbiotic relationship comes down to, spores in the vicinity of plant-roots being activated by chemical compounds excreted by the roots, however here the symbiotic relationship will be considered as a given and only the relationship from there on onwards is described.

‘The higher P_i uptake by mycorrhizal plants can be explained in terms of increased hyphal exploitation of the soil and the competitive ability of the hyphae to absorb localized and dilute sources of P_i’ (White and Hammond, 2008). When the fungus colonizes a plant-root, the fungus developes a special structure inside the infected cortical cell named an arbuscule. The exchange of mineral nutrients from the fungus to the plant and sugar-compounds from the plant to the fungus takes place at this arbuscule-cortical interface (Smith, 2000).

What is remarkable is that AM fungi actually down-regulate the uptake of P_i from the soil by the root itself once the plant has become mychorrhizal (Smith et al., 2003; Graham and Miller, 2004).

Cluster roots

Experiments with the model species white lupin (*Lupinus albus* L.) have shown that a lower concentration of P_i in the soil results in the development of proteoid roots, clusters of short lateral roots, which have the ability to differentiate quicker, stop growing after just a few days of growth and start developing large numbers of root hairs. This results in roots with a far superior P_i uptake potential than normal roots with indeterminate growth, it is also related to the larger amounts of organic acids that can be exuded from these clusters. These observations have also been made in Arabidopsis thaliana suggesting that this adaptation to P_i stress maybe widespread in the plant kingdom. (Lopez-Bucio et al., 2003).

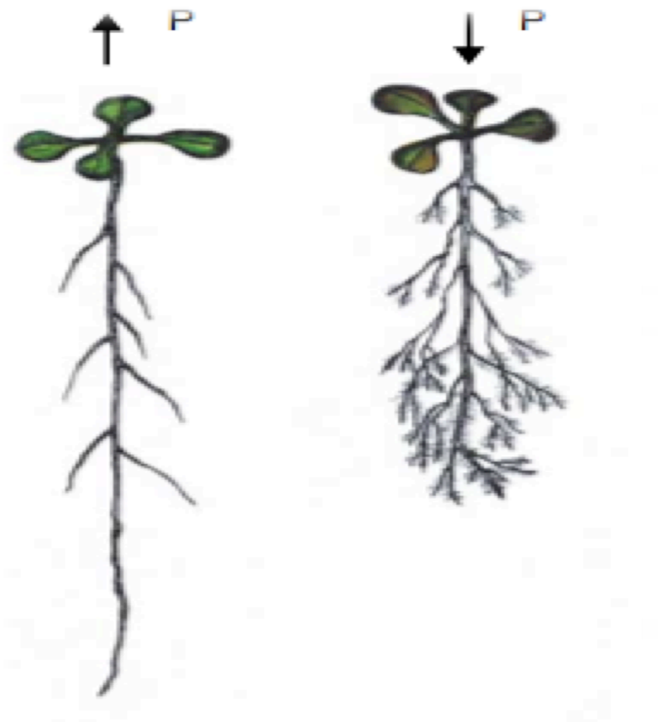

Fig. 3. Response of root system to hi - lo P_i in *A. thaliana.*

Root exudates
Plant roots can exudate different kinds of compounds with different purposes. They either contain signals that function as regulators for symbiotic microbes, influencing their growth and function. Or they influence the availability of nutrients directly via a direct chemical effect of the exuded compound.

Phosphorus in soil

- 'The soil is that weathered superficial layer of the earth that is mixed with living organisms and the products of their metabolic activities and decay.' -
(Odum and Barrett, 2004)

Properties of soil
In order to better understand the processes involved in the availability of P to the plant-roots, some knowledge of soil properties and processes, i.e. physical, chemical and biological is necessary.
Central to the following discussion about soil properties and soil-life should be the definition of soil quality:

- 'The capacity of a soil to interact with the ecosystem in order to maintain biological productivity, environmental quality and to promote animal and plant health.' –
(Doran and Parkin, 1994)

In the next paragraph the key physicochemical or abiotic properties are discussed starting with the most fundamental or leading in respect to other soil characteristics and building down to properties which are the direct consequences of these fundamental physical characteristics (adapted from Gobat et al., 2004)

Texture:
Is a stable soil property that only changes with long-term soil-development, it comprises:
- *mineral texture* relative proportions of sand, silt and clay determined by size of granules.
- *organic texture* sizes and texture of fibres and micro-aggregated matter.

The texture of any given soil determines its porosity and hydric regime, discussed below.
A more flexible/changeable soil property is ***structure,*** this mode of organization of solid constituents of soil, mineral and/or organic, changes for example with season. The proportion of micro- and macro-aggregates of mineral and organic particles determine the structure.

The texture and structure together are of great influence on the ***porosity and thus the hydric regime*** of soils. This is determined by the total amount of voids, in the soil filled with either water or air, these together represent the porosity. Although the total amount of water in these voids says virtually nothing about water availability, classifying the amount of water as dictated by the size-classes of the voids does. These size differences of the voids are relevant for plant roots because some voids and thus nutrients will only be reachable by the thinnest of root hairs or even only by fungal hyphae.

The most mobile and transient kind of soil water is *gravitational water*, this is only retained for a few hours or days after a rainfall. *Plant-available water* which is held by the meso-porosity of the soil (capillary porosity) from pores reaching from 0.2 to 50 uM, this water is available up until the wilting point where the root-sucking force is equal to the retentive force of the soil. *Plant-unavailable water* this is water retained in the finest pores, in films around particle surfaces or bound to minerals.

A very important attribute of a soil is the quality and composition of the ***clay-humus complex***. This is the meeting place of the organic and mineral 'worlds', a stable clay-humus complex promotes fertility of the soil by obtaining for it a few vital properties like an aerated structure and adequate water storage through flocculation of clay and humic colloids.

The clay humus complex slows down the mineralization of humified organic matter through the bonding of clay mineral-humus bonds this prevents leeching out of valuable nutrients. Because humus is bond to the clay, dispersion and thus clogging and compaction is being prevented. 'Formation and stability of the clay-humus complex depends on the quality and quantity of the organic matter' (Gobat et al., 2004) Cation exchange capacity (CEC) and 'base' saturation percentage CEC: 'Maximum quantity of cationic charges that a defined mass of soil can retain and exchange.'

Basic cation saturation percentage; 'Ratio between the sum of exchangeable basic (Ca^{2+}, Mg^{2+}, K^+ and Na^+ together form 99% of these) cations and the total cation exchange capacity.' It is a good measure of general soil development and it is correlated with pH. Undeveloped soils are more saturated and have high pH and vice versa. The pH and buffering power of a soil are important, because pH is an important determinant which influences the availability of elements for uptake from the soil-solution, conversely buffering power is a good measure of how stable a soil is.

Redox potential, a quantitative measure of the transport of electrons from donors to acceptors; which is directly linked to the amount of available oxygen in the soil air.

The interrelations of some of the above-described physicochemical properties are shown in Fig 5., where an arrow going from one box to another indicates that the former influences the latter. It becomes clear from this figure that the clay-humus complex plays a central role in functioning of the soil.

The soil solution, where the plant gets its mineral nutrients from is in constant exchange with the clay-humus complex. Because the soil solution is the only medium with which plant roots can exchange ions, the speed and direction of exchanges of ions between the clay-humus complex and the soil solution is very important for, among others, availability of P.

The processes of exchange between the solid materials of the soil – the clay-humus complex – and the liquid component of the soil – the soil solution are dependant on all the physicochemical properties of the soil previously discussed in this paragraph. But besides these abiotic factors a soil would not be the healthy system as described in the quote central to this chapter without a wide array of s**oil organisms.**

'An agricultural soil usually contains about 3000 kg of fresh-weight of soil organisms per hectare, an equivalent of 5 cows, 60 sheep or 35 farmers living under the surface'
(Bloem et al., 2006)

The three main constituents of total soil life are discussed below, selected by total biomass and relative importance in shaping the environment for the plant-roots, mammals i.e. burrowing animals such as rabbits, moles and other rodents are omitted.

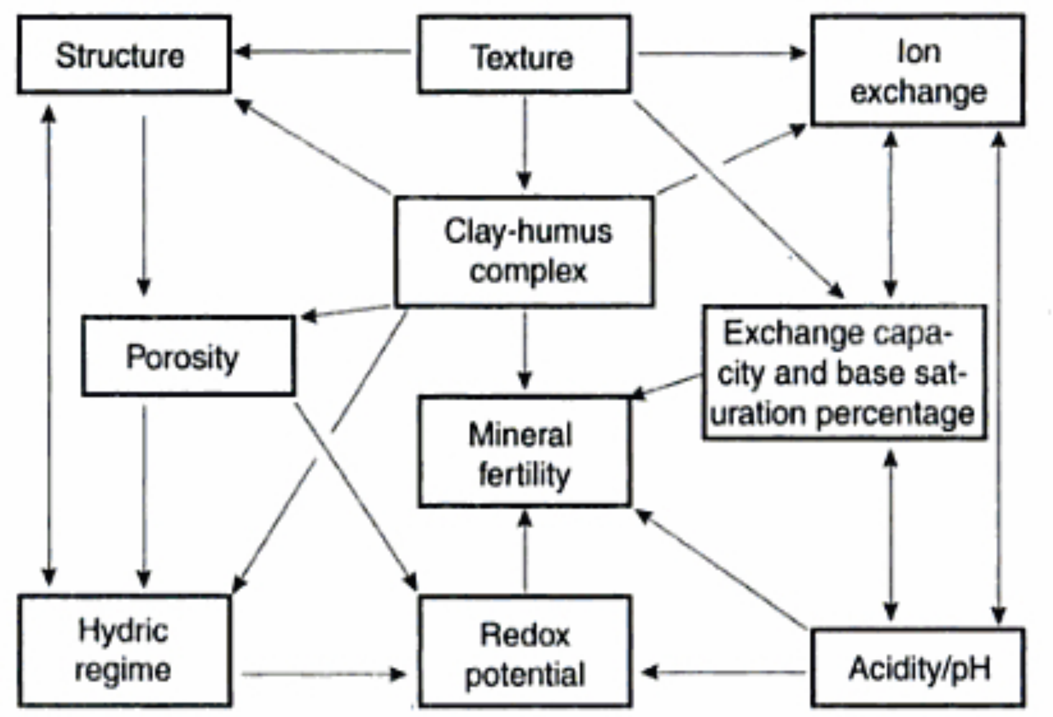

Fig. 5. Interactions between the various soil characteristics (Gobat et al., 2004).

Earthworms
Play an important role in altering the soil structure through ingestion and defecating - bioturbation - of the soil and directly influencing the properties of the clay-humus complex. Earthworms also break down plant debris into smaller pieces, by doing this, the surface area is greatly enhanced and fungi and bacteria can continue the process of decomposition.

Microorganisms; Bacteria and Fungi
Microorganisms influence the availability of P to higher plants in several ways i.e., by release of available inorganic phosphate through degradation of organic P compounds, by promoting solubilisation of fixed or insoluble mineral forms of P but also by immobilization of available phosphates by incorporating them into cellular material (Stevenson and Cole, 1999). So mineralisation, i.e. decomposition of organic materials for which microorganisms are well known and solubilisation make P_i more available, conversely immobilization makes P_i less available to plant-roots. The primary

mechanism by which microorganisms solubilize phosphorus is through the production of organic and inorganic acids. In this process the acid interacts with the phosphorus minerals replacing the metal ions with hydrogen atoms thus creating mono- or dibasic phosphates - $HPO_4{}^{2-}$ or $H_2PO_4{}^{-}$ - which are soluble. The solubilisation does not only benefit the microorganism that produces the acid to make P_i available for growth, but other organisms such as plants also benefit from the 'production' of the surplus P_i. Another mechanism of phosphorus solubilisation that occurs under reducing conditions such as in flooded soils is microbially mediated redox reactions in which iron oxyhydroxides and associated ferric phosphate (strengite) are reduced. 'In this process, dissimilatory iron reduction of ferric phosphates liberates soluble ferrous iron as well as orthophosphate associated with it.'(Mackey and Payton, 2009). Mineralization is the process that makes mineral nutrients available again in their inorganic form, by decomposition of plant and animal detritus. It is estimated that 70 to 80% of soil microorganisms are able to participate in mineralization of phosphorus through the activity of an array of enzymes, a diverse group of proteins referred to as phosphatases. These phosphatases can be categorized based on what type of carbon-phosphorus bond they break. (Mackey and Payton, 2009).

Immobilization is the process where labile phosphorus is removed from the reservoir of reactive phosphorus, this can occur in two different ways. Firstly by *transitory immobilization*, or cellular assimilation, this includes all processes where phosphorus is taken up into microbial cells and is rapidly reversible when these cells die. Secondly by processes that generate phosphorus containing minerals (Mackey&Payton, 2009).

Apart from the well-known mycorrhizae, which have already been discussed in the preceding chapter, other not in a root symbiosis living fungi, namely saprotrophic fungi play a crucial role in decomposing organic litter. All saprotrophic fungi produce extracellular enzymes that are capable of mineralizing C, N and P from soil organic matter and plant litter (Burke et al., 2010).

P forms in soil

The availability of P to plants varies with the form in which it is available in the soil. In Fig 1.3 total P is portioned into pools in accordance with the plant-soil-microbial interactions (Stevenson and Cole, 1999). As can be seen in the figure and as stated before, plants can only get minerals from the soil solution, so the way in which this pool is replenished is important for understanding mineral nutrition.

Most common forms of P available in the soil solution are $H_2PO_4^-$, HPO_4^{2-} en PO_4^{3-}, hereinafter all referred to as P_i (inorganic phosphate), see fig 1.4.

At any given time, a very small proportion of P is available in the soil solution, another 1-2% is in microbial biomass and >90% is in non-soluble fixated form. However the soil solution is in constant exchange with the labile P pool, which consists of a smallish fraction of the insoluble pool. This comprises the easily mineralized organic P and phosphates that are only very weakly adsorbed by clay colloids (Stevenson and Cole, 1999). Overall the capacity of a soil to supply the plants with a sufficient amount of P depends on:

- Amount of P_i in soil solution;
- Solubility of Fe-, Al- phosphates and P-hydrous oxides in acidic soils and on Ca-phosphate in calcareous soils;

- Quantity and fase of decomposition of organic residues;
- Activity of microorganisms (Stevenson and Cole, 1999).

Phosphorus in agriculture

'In agroecosystems, the farmer, is in a sense, the organism with the greatest impact on the environment in which the crops are grown' –
(Gliessman, 2007)

The main difference and at the same time main problem concerning agro-ecosystems compared to natural ecosystems is that in a natural system all the nutrients eventually get cycled back through the system, be it locally or globally.

Because farmers have to remove their harvest from their lands, nutrients are mined from the soils of the agro-ecosystems. And thus some form of fertilization is needed. It is useful to consider what conventional agricultural practice has been like up until now in respect to P_i fertilization of soils. Because P_i when applied to the soil is so easily fixated or leeched out and thus lost to the soil solution; farmers just over-apply it in order for a small portion to remain available for the crops. This results in a tremendously inefficient use of a scarce resource that, at the current rate will be depleted within eighty years. However as can be read in this paper the 'trick' to soil health and thus fertility is to build a stabile high quality organic matter fraction that steadily releases nutrients into the soil solution. A balance between what is taken up from the soil solution by the plants and what is released from organic matter is of vital importance in maintaining soil fertility over the years. Besides these basic chemical considerations it is important to note that with the application of a whole array of mineral fertilizers, soil life, which actually enhances fertility for 'free', is being killed.

Sustainable P_i application

Studies have shown that the application of organic farmyard manure and compost forms a good alternative for P_i fertilizers. (Sharpley, 1989; Hartikanen, 1989; Eichler-Lobermann et al., 2007; Gerke, 1994). Organic matter not only serves as a source of nutrients itself and improves the availability of P in a soil, it also enhances physical soil properties such as water retention, aggregate structure and stability. Because the humus content is increased microbial activity and thus natural release of mineral nutrients into the soil solution is improved (Frossard et al., 2002; Oehl et al., 2004; Oberson and Joner, 2005). Because of the before mentioned positive effects of a high soil organic matter content on natural processes that enhance the availability of mineral nutrients in the soil, extra mineral P application becomes unnecessary (Eichler-Lobermann et al., 2007). In this long-term study that was done in North-Eastern Germany for a period of 6 years the differences in both P-uptake by plants and P status of the soil between many different kinds of P application regimes was investigated. Although the highest yields were achieved when combining organic matter fertilization with spring supplied Triple Super Phosphate -TSP- this is not a sustainable solution for environmental reasons because of the high P surplus of over

100 kg ha^{-1} in 6 years time. The high soil P contents will in turn lead to higher losses of P from agricultural lands, and thus should not be recommended in the long term perspective (Eichler-Lobermann et al., 2007). From this same study it became clear that although there were differences in yields between treatments, there was only a weak correlation between total P application and total P uptake by the crops. This indicates that the amount of P in the soil was already sufficient to cover plant need. So in respect to P-nutrition organic fertilization can replace mineral-fertilizer application, provided that soil P contents are monitored accordingly so that in the long term P balance is sustained.

So although many positive results for a more sustainable use of managing soil fertility can be found, it is important to realize the extent of the consequences of business up until now. The crop-varieties currently used in agriculture have been bred in a period when mineral fertilizers were applied to a great extent and not much was tried to do in a sustainable way. This naturally results in varieties who might be considered lazy in some ways were their ancestors were more efficient. To take the example of mycorrhizal symbiotic associations which is initiated by a fungal spore detecting a signal from a susceptible plant root; when this plant root hasn't developed a pathway to give the required signal, no symbioses will come into being and seeds will have to be planted that have been artificially inoculated with the fungus.

Although this rather grim realization implies that plant scientists and breeders will have to 'start from scratch' at breeding crop species adapted to the specific demands of modern times sustainable farming practices while producing the biggest yields. It also means that farmers and researchers haven't scratched the surface yet of what genetic potential might be available in currently underappreciated crop strains.

The main sink for P_i is actually meat of animals that need to be fed *several times* the equivalent weight of end product in animal feed to produce one unit of actual meat. So obviously part of the solution would be to fertilize our lands not only with farmyard manure and compost but also with the final waste product of the meat industry, namely sewage sludge with human waste. Although the back cycling of P_i into the agro-ecosystems is of paramount importance in sustaining food production in the long term if we want to sustain a growing world population, it is not however the topic of this paper and the answer to an altogether different question.

Conclusions

Plants have evolved to grow and develop as efficiently, resilient and healthy as possible given the available nutrients and stressors, among other factors off course. When plants are under considerable, but not stunting, nutrient stress all available mechanisms to accumulate the necessary nutrients from the soil are used.

Man has developed methods to boost growth and development without, at first, a proper understanding of plant physiology and metabolism, or proper soil management. It turns out that when farmers 'over-fertilize' their lands that they not only shut-off a whole array of providing micro-organismal processes but also remove the incentive for the plant to 'work harder' for its mineral uptake. This results in a highly inefficient situation where the farmer has to compensate for the loss of efficiency by continuously applying readily available nutrients to the soil solution. Without proper understanding soil-P mechanics this is a waist of resources because the lion share of the applied minerals will not even remain available to the plants long enough. Nutrients eventually leach out or run-off into surface and ground water deposits, which is a serious environmental issue.

Part of the solution is to try to copy one of the very fundamental attributes of every ecosystem; the nutrient cycle. Although naturally a perfect cycle cannot be sustained, it can be done a whole lot more efficiently than it has been done up until now. As has been argued, sewage sludge, farmyard manure and compost all form good alternatives for the diminishing supplies of mineral fertilizers.

The main theme central to all soil cultivation in the mind of every farmer should be how to build and sustain a healthy and large organic matter content in his soils. So as to maximize the role of all the natural processes that take place in every healthy soil. Microbial activity promotion is a source, measure and a product of soil health. With this all attributes of a well balanced, properly functioning plant-soil ecosystem will return to the agricultural soils, despite cultivation.

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