

REVIEW

Improving the efficiency and effectiveness of global phosphorus use: focus on root and rhizosphere levels in the agronomic system

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Abstract Phosphorus (P) is essential for life and for efficient crop production, but global P use with limited recycling is inefficient in several sectors, including agronomy. Unfortunately, plant physiologists, agronomists, farmers and end users employ different measures for P use efficiency (PUE), which often masks their values at different scales. The term P use effectiveness, which also considers energetic and sustainability measures in addition to P balances, is also a valuable concept. Major physiological and genetic factors for plant P uptake and utilization have been identified, but there has been limited success in genetically improving PUE of modern crop cultivars. In maize, studies on root architectural and morphological traits appear promising. Rhizosphere processes assist in mobilizing and capturing sparingly soluble phosphate from rock phosphate. Combinations of phosphate-solubilizing microorganisms with ammonium-based nitrogen fertilizer, as well as strategies of fertilizer placement near the roots of target crops, can moderately enhance PUE. The desired concentration of P in the products differs, depending on the final use of the crop products as feed, food or for energy conversion, which should be considered during crop production.

Keywords acquisition efficiency, plant growth promoting rhizobacteria, phosphate, use efficiency, utilization efficiency

1 Introduction

Phosphorus (P) is an essential element for all living cells. In the lithosphere and the biosphere, almost all P atoms are covalently bound to oxygen, forming a pH-dependent

equilibrium of (hydrogen) phosphates. Via ester bridges with carbon or P atoms, various organic phosphates or polyphosphates rapidly form and are hydrolyzed during cellular metabolism, but sugar-phosphate polymers like DNA and RNA can be extremely stable, as evident from ancient DNA samples. Phosphorylation of sugars, nucleosides, other metabolites and proteins are major chemical modifications important in the basic metabolism of all living organisms that generate transient energy-storage compounds and add negative charges to a target compound. Finally, phospholipids are ubiquitous in cellular membranes and can only be partially replaced by glycolipids or sulfolipids, explaining why P is essential for life, including plants^[1]. Inorganic phosphoric acid/phosphate (P_i) and the various organic phosphate (P_o) forms (including monoesters, diesters and particularly the relatively inert phytate) have substantially different biological stabilities. Unfortunately, both P_i and P_o are chemically fixed, precipitated, occluded and adsorbed in a pH-dependent manner to soil Al^{3+} , $Fe^{3+/2+}$, Ca^{2+} oxides/hydroxides on particle surfaces and aggregates. This not only impairs the availability of soil phosphate for plants and microorganisms, but also poses difficulties for processing of the two macronutrients, P and Ca, within plant tissue. Similar problems apply for micronutrients such as Zn. Complex environmental factors determine the equilibrium between the different P-forms, as well as the mostly relatively slow conversion between them.

Plant roots respond to the difficulties in acquiring P by ramifying (changing root architectural and morphological traits, e.g., more dense, longer and thinner lateral roots, shallow root systems with preferential root development in nutrient-rich topsoil) to access a larger soil area and by chemical modifications of the rhizosphere, such as H^+ exudation for acidification, as well as exudation of sugars, organic anions, amino acids and secondary metabolites. Certain exudates, such as citrate and oxalate, have

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particularly high P-mobilizing activities, via ligand exchange, dissolution and occupation of P sorption sites, in which the precipitated metal oxides and hydroxides of phosphate interact with the organic anion thereby increasing the solubility of both P_i and P_o forms in the rhizosphere^[2–4]. Exudation of acid phosphatases from plant roots and root associated fungi, as well as alkaline phosphatases released from bacteria, can contribute to mineralization of soluble organic rhizosphere P, which is subsequently taken up by plant roots and soil microorganisms^[4,5]. Phosphate sequestered in the microbial biomass can be partially liberated into plant-available forms by the microbial grazers of the soil microfauna (protozoa and nematodes) via so-called microbial loop effects^[6]. Generally, however, P_i and P_o are sparingly soluble (P in typical agricultural soils is $< 10 \mu\text{mol}\cdot\text{L}^{-1}$) and sparingly mobile, especially at acidic and basic pH, which contrasts the high P_i and P_o mobility within plants^[7].

2 P efficiency and effectiveness

The majority of phosphate now enters the global P cycle from mining of rock phosphate (rock-P, mainly apatite, $\text{Ca}_5(\text{PO}_4)_3\text{OH}$) for producing readily plant-available P-fertilizers for agriculture (about 78% of mined rock-P), a highly inefficient process^[8]. High quality rock-P resources used for fertilizer production are limited, globally concentrated and chemical conversion to readily plant-available P is energetically costly. Agronomy focuses on how to fertilize crops optimally with P, but this neglects how the plant products are ultimately used. Especially for multipurpose crops, such as maize, where distinctly different amounts of P may be desired for human food, different types of animal feed and energy conversion, much of the harvested P will be unused. This excess P ultimately ends up in human urine and excreta, manure, digestates, plant residuals, industrial and household wastes and in the environment, from which P, in principle, could be efficiently recycled, but currently is not^[9]. The efficiency of P flow in the agronomic part of this nutrient cycle is often given as the P use efficiency (PUE) and indicates the fraction of harvested P from the fertilizer P applied, which rarely exceeds 30% in real production systems and typically is closer to 15%–20%. PUE can also be defined as $1 - (\text{sum of losses} / \text{inputs}) \times 100\%$ and reflects exclusively the P mass balance. However, mass balances do not consider the effectiveness of a nutrient within a global cycle, e.g., whether high quality food is efficiently produced and consumed, whether or not it is wasted and efficiently contributes to feeding the world population (and contributes to well-being). Obviously, inefficient P use with little recycling and huge losses (e.g., by the consumer) cannot be considered sustainable, but even if small losses occur, the ecological footprint may be high, as the energetic requirement to obtain acceptable P

balances is excessive. Thus, effectiveness of the energy flow within a nutrient cycle at a certain P level should also be considered, even which type of energy, e.g., solar vs fossil fuel impacts P effectiveness (PE). All these factors can be considered by an efficiency sustainability factor (ESF), which is set to 1 for an ideal, sustainable system in which the genetic potential of all organisms is optimally used. The global P cycle effectiveness can thus be defined as $\text{PE} = (1 - (\text{sum of losses} / \text{inputs})) \times \text{ESF}$. Conversion of rock-P and chemical processing to convert it to plant-available P decreases ESF and agronomic systems that efficiently utilize rock-P and P forms from products of waste recycling instead of soluble P-fertilizer would be more sustainable. Clearly, transportation and local recycling are taken into account in this sustainability factor and these must ultimately be weighted based on their energetic effects. Unsustainable transport of P in plant products (e.g., feed legumes) across continents and the inefficient use of P in current meat-dominated diets in developed countries, overeating and excessive household food waste are obviously relevant and must also be considered. We estimate that country-specific PE, when calculated by such an equation, ranges between 0.1 and 0.5, but more detailed parametrization of losses and the sustainability coefficient is required. Efficiency of the global cycle is thus improved by reducing P losses to the environment, but also by increasing the effectiveness of using P within individual processes in the global P cycle.

3 P utilization efficiency of plants

A minimum of roughly 2–3 $\text{g}\cdot\text{kg}^{-1}$ P in shoot dry mass of most crops is needed for the production of near-optimal biomass and yield, while some specialist plants that are adapted to low-P soils maintain only around one-tenth of that P concentration in their shoot biomass, e.g., some Proteaceae^[10]. Such specialist plants not only utilize P most efficiently in their cellular metabolism, but also adjust their development accordingly, allocate their reserves specifically to critical (young) tissues and efficiently transferring P from senescing tissues. They acquire P often efficiently by a combination of massive organic anion release in root zones for maximal growth, occasionally in cluster roots (brush-like dense lateral roots of limited length on first order laterals, covered densely with root hairs) or dauciform roots^[10]. However, the genetic potential to rapidly produce biomass and grain of such specialist plants is relatively low compared to current crops. A meaningful P utilization efficiency (PUE) of specialist plants and crops is defined as $\text{PUE} = \text{grain yield} / P_{\text{shoot}}$ (or = $\text{biomass} / P_{\text{shoot}}$), with P_{shoot} the total amount of P accumulated in the shoot (i.e., the P content). Obviously, a cellular metabolism that builds up more grain per P_{shoot} is more efficiently utilizing P. Indeed, disregarding the harvest index (the fraction of the shoot biomass that

ends up in grain yield is maximally close to 0.75 in common wheat and 0.5 in maize), PUE is essentially the inverse of the shoot P concentration ($PUE = 1 / [P_{\text{shoot}}]$).

It should be noted that the term “P concentration” in agronomy and plant nutrition has a different meaning than in biology and physiology. In the latter case, the concentration describes the molarity, how many moles of P_i are dissolved in a liter of water. Elemental P, however, is never found dissolved in water in biological systems. In plants and soil solution only phosphoric acid or hydrogen phosphate ions are found, and P is not reduced after uptake by the plant. In agronomy and plant nutrition, the P concentration gives the mass fraction of elemental P with respect to total dry biomass ($\text{mg} \cdot \text{g}^{-1}$ or ppm), which has the advantage that this value is directly given by analytical equipment, such as atomic absorption spectroscopic elemental analyzers, or ICP-MS or ICP-OES machines, simplifying the processing of the nutrient values. P fertilizers, by contrast, are sold in quantities of P_2O_5 (45.2% P), somewhat reflecting the fact that phosphate is the active component of the element P, although a chemical equivalent to P_2O_5 does not exist. For a better PUE of the entire agricultural system, it would be helpful if all those involved could harmonize their units and efficiency measures.

The genetic potential of the crop sets an upper limit for grain, fruit or biomass yield. Crop genetics also sets the minimal level of P in the tissue required for accumulation of biomass, so the plant acquires phosphate from the soil that is sufficient for cellular function and growth. There is no sharp threshold below which plant metabolism is limited by P, but an increase in tissue P (luxury P) gradually reduces P efficiency, as other factors become limiting. A meaningful critical P tissue level for individual crops sets a threshold where the crop is able to reach 95% of its genetic potential for yield. Plant-mobile phosphate is fractionated and allocated to the most demanding tissues and compartments. Photosynthetically active young leaves and their chloroplasts, as well as root meristems and young growing roots require the highest amounts of P. When P is abundantly available, plants acquire luxury P, which is mostly stored in the vacuole. Loss of a vacuolar P_i transporter in *Arabidopsis* leads to severe growth defects at higher external P_i supply, as excess P_i cannot be separated from the metabolism in the cytosol, which may interfere with the metal homeostasis, but these plants are similar to the wild type at very low external P_i ^[11]. Notably, vacuolar P_i is strongly depleted in another mutant with reduced expression of *PHO1*, a gene that participates in the root to shoot translocation of P_i . This mutant maintains maximal shoot growth similar to P_i -sufficient plants despite being P_i -deficient and suppresses the gene expression profile normally triggered by P_i deficiency. Obviously, reduction of growth rates represents a highly regulated adaptive response to limitations of nutrient availability, as previously shown for N limitation^[12], which acts long before

the appearance of nutrient limitations for physiological processes. The finding that inositol polyphosphates act as signaling molecules that regulate the P_i homeostasis via interactions with SPX protein domains, which are found in P_i transporters, P_i -regulated enzymes, and signaling proteins, further suggests that genetic manipulation of crops via targeting the P_i -sensing components may become possible in the future^[13]. Inositol polyphosphates decreased under P_i starvation, liberating a transcription factor that promotes the P_i -starvation gene expression cascade, which is generally suppressed at sufficient P_i ^[13].

4 P uptake efficiency and P use efficiency concepts for crops and agronomic systems

The nutrient use efficiency concept, with $PUE = \text{yield} / P_{\text{soil available}}$, combines several easily measurable components that make sense for individual plants or plant communities per unit area in the field. Separation of this term into meaningful components was initially proposed and discussed for nitrogen^[14,15], but the biological meaning is universally applicable to all elements, including P. PUE equals the product of PUE (explained above) and P uptake efficiency (PUpE), $PUpE = P_{\text{shoot}} / P_{\text{soil available}}$, thus $PUE = PUpE \times PUE = P_{\text{shoot}} / P_{\text{soil available}} \times \text{yield} / P_{\text{shoot}} = \text{yield} / P_{\text{soil available}}$. Both components of PUE can be genetically improved, although they are not completely independent of each other. The shoot P concentration is a valuable indicator of the plant P status, but it fails to indicate how efficiently a plant genotype acquires P. For example, barley and maize mutants lacking root hairs that are considered critical for taking up P in low fertile soils, were not affected in their tissue P concentrations, but P concentrations were reduced with less available P in the soil and under drought conditions^[16,17]. Thus, root hairs matter for the shoot P content, rather than the P concentration, when plants are grown in P-deficient soil^[16,17]. This can be explained by the PUE concept, where PUpE reflects the uptake and capture of P_i , which is evidently expected to be affected by root hairs, while PUE is only slightly affected by loss of root hairs as PUE accounts for the assimilation and translocation of P that has already been taken up.

Given the large quantities of fixed, not easily available P in many agricultural soils, plant-available P is still not easily predicted by a single wet extraction quantification method. Many extraction methods (such as Olsen-P and Bray-P) are valuable and often give a reasonable estimate of P availability for the majority of soils, but none of the available methods can reliably estimate plant-available P in all soils. Country-specific P extraction protocols have been put in place by some governments, further complicating global comparisons.

For farmers, the most immediate goal is the yield gain from fertilization (yield increase relative to unfertilized

yield, i.e., Δyield), considering that residual P soil from previous fertilization can often adequately support plant growth for several growing seasons. This is defined as $\text{PUE}_{\text{farmer}} = \Delta\text{yield} / \text{P}_{\text{fertilized}}$, but this neglects fertility maintenance considerations, which are better supported by farm gate balances, for which appropriate legislation is useful. Political intervention is also needed to prevent excessive regional aggregation of animal farming, as long-distance transport of organic waste P is uneconomic and drives serious P imbalances in such regions.

5 P efficiency: do we want high P in grain?

The agronomic concept of PUE, discussed above, neglects the specific requirements for P in the end use of the grain or biomass produced. Phytate, an inositol polyphosphate, is predominantly present in the vacuole and accounts for up to 80% of the P in grain crops. It cannot be digested by humans and non-ruminant farm animals, so most phytate-P is excreted without using the P present in the molecule. Although P stored in grain supports seedling development for about 2 weeks, the optimal P content of grain needed for successful establishment in the field are often unclear^[18]. Low-phytate mutants of maize and other crops have similar total seed P content, but a somewhat reduced agronomic performance^[19] and reduced stress resistance during seedling establishment^[20]. Phytate precursors have multiple roles in cellular metabolism (maybe even in phosphate signaling) and especially in plant development, so genetic modification to reduce seed phytate is likely to have negative secondary effects^[20]. Given that high phytate concentrations in seeds is universal within the plant kingdom, both in wild and domesticated species, its physiological and ecological functions are likely to be significant. Phytate additionally chelates essential metals, reducing their bioavailability, thus low-phytate agriculture could, in addition to reducing unused P loads in food, feed and excreta, have beneficial effects on micronutrients in animal and human diets^[19].

6 Resource allocation to improve P acquisition and root structure

An increased P_{shoot} (resulting primarily from more biomass) indicates that the efficiency of acquiring P has increased, given that $\text{PUPE} = \text{P}_{\text{shoot}} / \text{P}_{\text{soil available}}$. This results from plants producing more roots, which is driven by resource allocation (mainly sugars and amino acids, but also P) to growing root tips and the regions of branching points. The complex interplay between the phytohormones auxin and cytokinin, in addition to gibberellin, ethylene, brassinolides, jasmonic acid, strigolactone, abscisic acid and probably other hormone-like signals, such as nitric oxide and signaling peptides, is crucial for determining

resource allocation. Auxin appears to have a major, if not dominant role in regulating this resource allocation. During vegetative growth, allocation to either the roots or to the shoot is reflected in the root: shoot ratio, which decreases with plant age and is typically in the range 0.45–0.15 for major crops. Moderate nitrogen and P deficiency, as well as moderate water shortage, substantially increase this ratio, so that plants put more photosynthates into roots and less into shoot growth. As a consequence, overall photosynthesis and carbon gain is reduced, ultimately reducing root growth. In maize, overexpression of the auxin-responsive auxin efflux carrier gene *ZmPIN1a* (which is responsible for the basipetal auxin flow from the shoot to the root tips) increased the root: shoot ratio of transgenic plants, stimulated lateral roots while shortening them and impaired shoot elongation^[21]. These changes mimic the physiological responses that occur under low P and as a consequence, densely grown plants in the field had higher yields and better performance in a low P environment. In rice, loss-of-function mutants of *OsARF12* (encoding an auxin responsive factor) reduced primary root length, but stimulated lateral number^[22]. These mutants were more responsive to low P and intrinsically had an upregulated transcriptional low-P response, leading to substantially increased P concentrations in their leaves, suggesting that *OsARF12* is a negative regulator of the low-P response^[22].

Among the major crops, maize, wheat and rapeseed with fibrous root systems respond to low soil-P availability by altering root size and architecture, while legumes tend to modify the chemistry of the rhizosphere^[23]. Often, the specific root length (root length / dry mass) increases under P-deficient conditions, leading to thinner roots, in addition to more root branching and more dense and long root hairs. Notably, long and dense root hairs are typically found in non-mycorrhizal crop species such as rapeseed, while mycorrhiza, and the potential to form mycorrhiza, apparently shorten root hairs (e.g., in maize and wheat), indicating a similar role for both fine structures to penetrate into soil pores for uptake of water and soil-immobile nutrients^[24]. Mycorrhization in major crops is favored by thicker roots and major crops substantially differ in their root characteristics, suggesting that each trait also comes with a trade-off^[25]. Root hair length can be easily measured in undisturbed 2D setups like rhizoboxes, minirhizotrons, root windows or in soil-free systems^[26], and it has been found that their length and regulation by nutrients strongly depends on the system in which they are grown^[27]. In compressed soil, where mechanical constraints limit root and root hair elongation, these may invariably be relatively short, irrespective of large differences in the genetic elongation potential of the crop under study.

Root branching not only increases the root surface, enabling the plant to access greater soil volume, it is most useful in the topsoil, where most of the soil-immobile fertilizer P is located^[28]. However, the topsoil dries out

quickly so that roots in this layer may provide limited support for plants under dry conditions.

Plant breeders have altered root architecture and morphology to improve PUE in crops^[21]. Using a maize recombinant inbred line (RIL) population, the genetic relationships between root architecture and PUE uptake efficiency have been established. QTL-based selection for root traits allows higher PUE cultivars to be developed^[23]. Major rice QTLs responsible for improved P acquisition via improved rooting under low P supply have been identified in rice and the underlying gene encodes a protein kinase, the P-starvation tolerance 1 (PSTOL1)^[29]. Beneficial alleles of *PISTOL1* were identified in landraces originating from regions with poor soils, suggesting that exotic germplasm is a valuable genetic resource for low P adapted genotypes. Beneficial *PISTOL1* alleles, however, increased rooting irrespective of P supply (in low and high P availabilities)^[29]. Several *PSTOL1* homologs were found in maize and QTL mapping suggests that these also have a prominent role for root traits and PUE under low P supply^[30,31]. However, many more loci have been identified that are also beneficially associated with superior PUE, but most of these have not been fully characterized genetically^[32–34].

7 Rhizosphere processes and manipulation by microbial inoculations

The rhizosphere, the plant-influenced soil close to the root surface, is depleted from sparingly soluble, soil-immobile nutrients, such as phosphate, when plant demand is high. Generally, the microbial activity in the rhizosphere is increased compared to the bulk soil due to the release of low molecular weight carbon compounds from the roots. Although microbial diversity is reduced, a fraction of microorganisms massively benefits from these plant exudates^[35]. Exudates are mostly released from a zone just behind the root tips, where roots are most active and the vascular system starts to differentiate, the Casparian strip is just being built and nutrients are taken up. Part of this release may be passive loss mediated by diffusion from the not fully differentiated root tip and its developing vascular system (open vessels), but the amount and composition of this release is highly regulated, e.g., by the nutritional and health status, suggesting a beneficial role for this carbon release despite the massive loss of fixed carbon and energy. Typically, the carbon release via low molecular weight compounds maximally amounts to less than a few percent of the photosynthetically fixed carbon, while root respiration may be responsible for much higher carbon loss, up to 40% under unfavorable conditions^[36]. One reason why the release of sugars, amino acids or organic acids may be beneficial is the control of pathogenic microbes, such as the fungus *Rhizoctonia solani*, which can be suppressed by beneficial rhizosphere commu-

nities^[37] that are promoted by exudate patterns in accordance with their substrate requirements. Various studies now suggest that phenolic compounds and other secondary metabolites are selectively released by plant roots as allelochemicals and phytoalexins and alter rhizosphere microbiome composition^[38]. Their release is stimulated after contact with pathogens, further supporting an active role of the plant in releasing this carbon primarily as a defense strategy^[39]. The antioxidant and chelating properties of phenols primarily impact on the metals in metal-phosphate complexes, thus indirectly contribute to P mobilization^[40].

Plant-growth promoting effects of microbial and non-microbial inoculants are more promising at moderate P level than at very low and high P levels, as evident from a meta-analysis^[41]. It is, however, possible that there is substantial publication bias in such data, as successful PGPR-effects are much more likely to be published than unsuccessful experiments. Indeed, in a recent collaborative EU-funded project in which the suitability and economic feasibility of many biostimulants were tested, crop growth-promoting and/or yield-increasing effects of microbial inoculants were found in only about 30% of several hundreds of experimental variants. The vast majority of the tested biostimulants had previously been shown to be beneficial for P usage in plants and their selection was based on sound literature evidence. In other words, growth stimulation was absent in the majority of cases (in 70% of experiments) and was less frequently observed in the field compared to greenhouses^[42].

Certain production systems (e.g., tomato production systems based on nursery production in greenhouses with organic fertilizers and low fertility drip-fertigated field with mineral fertilizer in the Negev Desert) strongly respond to microbial inoculants with improved phosphate acquisition, quality and yield^[43]. Beneficial effects of consortia inoculation vs single strains have also occasionally been observed, e.g., in a low fertile soil, where the soil microbial community is profoundly changed by inoculation of consortia^[43]. Despite substantial rhizocompetence of inoculated microbes, these mostly represent a minor fraction of the soil microbiome after a few weeks, however, and community shifts toward less potentially pathogenic composition can persist beyond the prominent presence of inoculants^[44]. Mycorrhizal associations are often increased due to larger roots and more infection sites, but the mycorrhization density was not increased^[44]. Consistent with the PUE concept (described above), inoculants typically do not increase shoot P concentrations and PUE, but rather increase the P content and PUE.

A major option for improving global PUE is recycling, but many recycled-P fertilizers (such as incineration ashes) do not deliver readily plant-available P and this is rarely improved by combination with microbial inoculants^[45]. However, maize growth benefited from some organic P-fertilizers, such as composted manure, in combination with

several microbial inoculants, and PUE was improved^[45]. Mechanistically, most microbial inoculants, irrespective of whether these were fungi or bacteria (Gram-positive and Gram-negative), similarly appeared to promote root growth (and, as a consequence, shoot growth), rather than having major stimulatory roles in P solubilization or P mobilization^[43,45]. Furthermore, microbial community shifts toward more beneficial microbes probably allow plants to direct fewer resources to defense, having less trade-off for growth. It is important to note that within the entire Biofactor project, crops grown under optimal nutrient supply without any stress never benefited from biostimulants, suggesting that only stressed and nutrient-limited plants benefited from the inoculants via relieving the growth suppression through phytohormonal actions. Microbial inoculants, if effective, thus recovered part of the genetic potential of plants under mild stress. Their usefulness and effectiveness in agriculture systems therefore appears restricted^[42].

8 Rhizosphere management by ammonium-based fertilizers

As crops require both P and nitrogen in large amounts, ammonium-containing organic or inorganic P-fertilizers, in which ammonium is either stabilized by the addition of a nitrification inhibitor or locally applied at high rates, have been used for induction of rhizosphere acidification. This helps to dissolve P from rock-P and other acid-soluble P fractions in soils. Since the potential ammonium-induced acidification of single plant roots is frequently limited by the high pH buffering capacities in alkaline soils^[46], placement of ammonium fertilizers with the ability to trigger local root proliferation in nutrient-rich patches has been employed to spatially increase rhizosphere acidification. Placed ammonium-induced root clustering, which was sufficient to promote P solubilization even in soils of pH > 8^[47]. Phosphate solubilization from rock-P in the rhizosphere is highly attractive, as the chemical conversion to plant-available P is then performed by the plant–soil system, rather than by energetically costly processes by the fertilizer industry prior to its application. Solubilization of rock-P, moderately aided by various microbial inoculants, was possible in soils of low and high pH (Fig. 1(a)), but did not efficiently work in calcareous soils with strong buffering capacity in maize^[48]. Rhizosphere acidification was the major driver to increase PUE, while microbial inoculants, despite having phosphate solubilizing properties, mostly contributed indirectly by root growth stimulation^[49]. Rhizosphere P-mobilizing enzymatic activities, such as alkaline phosphatases, were only marginally increased by inoculants in tomato^[44] but may be beneficial in the presence of higher concentrations of soluble organic-P forms (e.g., after application of organic fertilizers). However, their general contribution to PUE appears to be

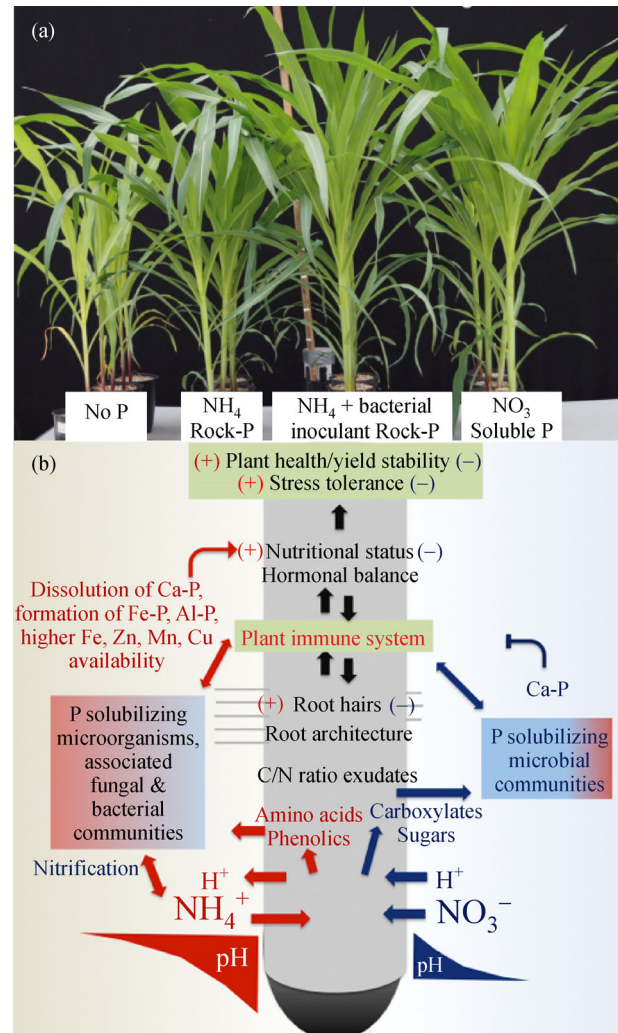


Fig. 1 Increased availability of sparingly soluble P-fertilizer for plant growth by ammonium-based fertilizer and microbial inoculation. (a) Maize shoot growth improvement by stabilized ammonium fertilizer in combination with rock-P on a fertilized calcareous alkaline subsoil (pH 7.6) mixed with sand (30%). From left to right: no rock-P (but all other nutrients, nitrogen as NO₃⁻), stabilized ammonium with rock-P, stabilized ammonium with rock-P and bacterial inoculant (a *Pseudomonas* strain), soluble P with nitrogen as NO₃⁻; (b) scheme of nitrogen form-associated changes in the root physiology and rhizosphere, which in the case of ammonium-induced acidification help to transiently dissolve P_i from rock-P (apatite), before it is again fixed to Fe-P and Al-P. Possible rhizosphere effects on soil chemistry, microbiome and availability of nutrients are indicated (photograph courtesy of Isaac Mpanga).

minor. In contrast, rhizosphere acidification has secondary benefits for acquisition of micronutrients (Fig. 1(b)) connected with improved biotic and abiotic stress tolerance^[50,51]. A distinctive root exudation profile with more amino acids and fewer organic anions is expected with ammonium compared to nitrate, as direct ammonium assimilation in the roots consumes organic acids, potentially shifting microbial communities toward more

favorable compositions and additionally aiding plant health^[52]. Therefore, aiding solubilization of rock-P is not the only useful effect of ammonium-containing P-fertilizers. Also recycling fertilizers like struvite (an ammonium magnesium phosphate) have outstanding P-fertilizer properties in many soils.

9 Field and plot level: plant cooperation

In maize breeding, much of the yield increase per unit area over the last century came from higher yield responses at high nutrient availability attained at increased planting density^[53]. These responses were associated with moderate changes in the root architecture. Clearly, this kind of PUE increase cannot be determined by individual plant screening but requires research with plant communities in the field. Co-cultivation of maize with legumes, such as bean, substantially increased usage of P by maize via interactions of the roots of both crops^[54], but mechanization of the management of such co-cultivation systems remains technically challenging. Although crop rotations with legumes are common in low-input farming systems, low legume yield and fertilizer prices make this less attractive to farmers in many developed countries. Most crops are currently grown in large monocultures with variable overlap in the P extraction capacity that stems from seeding density and overlapping soil extraction zones. In maize, wheat and rice, the large distance between the rows ultimately leads to little overlap and little competition for P (as roots seldom meet). With maize, however, undersown catch crops or co-grown legumes may mobilize P and positive effects on the PUE are common. However, co-cultivation systems have technical difficulties at harvesting time, such as separation of harvest products and limited phytosanitary (herbicide) options.

10 Conclusions and perspectives

There is much room for improving the PUE and use effectiveness within the global P cycle. This includes plant genetics, root and rhizosphere traits, which can be improved by breeding and management. However, a holistic view on the losses of P in the system, especially those from (human) wasting at various levels, is required to optimize use and effectiveness of the limited resource P.

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Compliance with ethics guidelines Uwe Ludewig, Lixing Yuan, and Günter Neumann declare that they have no conflicts of interest or financial conflicts to disclose.

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