

Opinion

Tightening the Phosphorus Cycle through Phosphorus-Efficient Crop Genotypes

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We are facing unprecedented phosphorus (P) challenges, namely P scarcity associated with increasing food demand, and an oversupply of P fertilisers, resulting in eutrophication. Although we need a multidisciplinary approach to systematically enhance P-use efficiency, monodisciplinary studies still prevail. Here, we propose to tighten the P cycle by identifying P-efficient crop genotypes, integrating four plant strategies: increasing P-acquisition efficiency, photosynthetic P-use efficiency and P-remobilisation efficiency, and decreasing seed phytate P concentrations. We recommend P-efficient genotypes together with diversified cropping systems involving complementary P-acquisition strategies as well as smart P-fertiliser management to enhance P-use efficiency in agriculture dependent on soil P status. These strategies will reduce P-fertiliser requirements and offsite environmental impacts, while enhancing seed quality for human and livestock nutrition.

Tightening the Phosphorus Cycle for Sustainable Food Security

P is essential for all life on Earth. Increasing global food demand and the emphasis on high crop yield have substantially increased the use of **rock phosphate** (see [Glossary](#)) for the production of P fertiliser [1]. Rock phosphate reserves are expected to be exhausted in the next 50–100 years [2,3]. In addition to the diminishing phosphate rock reserves, the decreasing quality, geopolitically uneven distribution of rock phosphate reserves, as well as increasing phosphate costs, have exacerbated the concerns [1,4].

Excessive use of P in agriculture has led to the accumulation of soil P in intensively managed croplands and grazing systems, leading to P losses via runoff, leaching and water erosion, causing eutrophication of surface waters [5,6]. Wind erosion also contributes to eutrophication of terrestrial natural systems [7]. Thus, it is critical to manage P reserves more judiciously. Current research focusses on monodisciplinary strategies to enhance P-use efficiency. It is increasingly acknowledged that adopting a multidisciplinary approach is crucial to tighten the P cycle [8]. Here, we focus on the plant aspect and propose four strategies to tighten the P cycle in cropping systems, with three strategies focussing on exploring the genetic variation in **P-acquisition**, **-use**, and **-remobilisation efficiency**, and one emphasising the importance of low total P and **phytate** P concentrations in seeds used as food and feed ([Figure 1](#), Key Figure). These strategies will have profound implications for the P cycle, including animal-production systems and human consumption, together leading to reduced requirements of P-fertiliser input, enhanced **micronutrient** availability of food and feed, and decreased P-related environmental pollution.

Four Strategies of Phosphorus-Efficient Genotypes of Cereals and Grain Legumes

Phosphorus-Acquisition Efficiency

Soil contains large quantities of P, yet most of this is not available to most crops. Much progress has been made to enhance crop P-acquisition efficiency through root

Highlights

Adopting a multidisciplinary approach is crucial to tighten the P cycle; however, current research still focusses on monodisciplinary approaches.

Crop genotypes with high efficiency of P acquisition, photosynthetic P use or P remobilisation, or low seed phytate P concentrations are crucial to reduce P-fertiliser input and P-related environmental impact and to enhance micronutrient availability of food and feed.

While native plant species differ substantially in their strategies for P acquisition under low P availability, there is also considerable genotypic variation in P-acquisition strategies in crop species and genotypes.

At the leaf level, P is preferentially allocated to photosynthetic cells to enhance photosynthetic P-use efficiency, while, at the cellular level, plants maintain a higher ratio of metabolic P to lipid P, and function at very low levels of ribosomal RNA.

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foraging strategies and P-mining strategies [9–11]. These strategies are closely related to root traits, ranging from architectural traits (shallower root growth angle, more adventitious roots, and lateral branching), to morphological traits (thinner and longer roots and more root hairs), physiological traits (greater release of organic anions and phosphatases) and symbiotic traits (associations with mycorrhizal fungi and P-solubilising bacteria) [12–14].

While native plant species differ substantially in their strategies for P acquisition under low P availability [15], there is also considerable genotypic variation in P-acquisition strategies for several crops [16,17]. For example, the concentration of **rhizosheath carboxylates** varies substantially among chickpea (*Cicer arietinum*) accessions [11], while common bean (*Phaseolus vulgaris*) and maize (*Zea mays*) exhibit a large genotypic variation in adventitious root formation, lateral root development, and root hairs [18,19]. Moreover, traditional rice (*Oryza sativa*) cultivars with greater root length and early root growth regulated by protein kinase PSTOL1 could also act positively on plant P uptake, contributing to enhanced P acquisition [20]. These differences in P-acquisition modes may be partly attributed to the trade-offs between carbon cost for different P-acquisition strategies [21].

In addition to plant strategies, associations of plants with soil microbes, such as **arbuscular mycorrhizal fungi** (AMF), **ectomycorrhizal fungi**, and P-solubilising bacteria, can significantly enhance crop P-acquisition efficiency [12,22]. For example, maize-associated mycorrhizal fungi release fructose and trigger P-solubilising bacteria, which mineralise phytate [23]. Depending on plant species, genotypes have different capacities to shape their **rhizosphere** microbial communities [24]. Future work should focus on the genotypic variation in crop species in root-associated microbial strategies, using an easily measurable proxy, such as leaf manganese concentration for carboxylate release [15] or blumenols as shoot marker for root symbioses with AMF [25,26].

Agricultural intensification is often practiced in highly **P-sorbing soils**, such as acid soils reported in Chile [27] or calcareous soils in South Australia [28]. Despite high total P levels of such soils, P availability is often low, because P is bound to mineral complexes [such as (hydr)oxides of iron and aluminium, and calcium], rendering P poorly available. To overcome P limitation for crop growth, P fertiliser has often been overapplied, causing soil total P surpassing the inflexion point, after which plant-available soil P increases dramatically, leading to a greater likelihood of P losses [29].

We propose using efficient root foraging or P-mining genotypes in combination with agronomic strategies to enhance P acquisition from agricultural soils varying in soil type and soil P status (Figure 2). If the total P concentration of a soil is lower than the inflexion point, we recommend selecting genotypes with high soil P-mining capacity (such as greater carboxylate and phosphatase exudation, or association with AMF) to enhance soil P acquisition [11,30,31]. In addition, other strategies, such as **intercropping** or rotating crop species with strong P-mining capacity or providing a localised supply of starter P fertiliser close to roots, are also effective measures for efficient P acquisition [32,33]. After the inflexion point, selecting crop genotypes with high root foraging capacity (such as more adventitious roots, lateral branching, or deep roots), or growing P-demanding crops in intercrops or rotations to enhance P uptake can significantly reduce P-fertiliser input and P losses. These strategies are especially important in soils with higher residual soil P stocks [34]. In summary, crop genotypes hold huge potential in enhancing P-acquisition efficiency in agriculture.

Glossary

Arbuscular mycorrhizal fungi (AMF):

a group of fungi that form symbiotic structures referred to as arbuscules (highly branched exchange structures) within root cortical cells.

Carboxylate: carboxylic acid minus its protons; organic anion.

Ectomycorrhizal fungi: a group of fungi that form symbiotic structures in which a large part of the fungal tissue is found outside the root.

Facilitation: positive effect of one plant on another.

Intercropping: one crop plant grown in combination with at least one other crop on the same plot at the same time.

Micronutrient: essential inorganic nutrients that are required in relatively small quantities. In order of decreasing amount needed, these are iron, boron, chlorine, manganese, zinc, copper, molybdenum, and nickel.

(Nutrient) acquisition: a process by which plants mobilise and take up nutrients (e.g., P) from the surrounding environments.

Phospholipid: major category of membrane lipids, generally comprising two fatty acids linked through glycerol phosphate to one of a variety of polar groups.

Phosphorus-sorbing soils: soils that strongly bind P in a manner that makes P poorly available to roots and microorganisms.

Photosynthetic phosphorus-use

efficiency (PPUE): rate of photosynthesis per unit leaf P.

Phytate (-hexakisphosphate): salt of inositol hexakisphosphoric acid. myo-Hexakisphosphate is a major organic P-storage compound in seeds. Inositol hexakisphosphate can also be a major fraction of organic P in soils, accounted for by four stereoisomers, *myo*, *scyllo*, *neo*, and *D-chiro*. The origins, dynamics, and biological function of the three stereoisomers that are not found in plant seeds remain unknown.

Remobilisation: export of nutrients and soluble organic compounds from senescing organs during senescence.

Rhizosheath: soil adjacent to the root that can be physically collected.

Rhizosphere: zone of soil influenced by the presence of a root; the size differs for different molecules, being smaller for phosphate and larger for nitrate and water.

Photosynthetic Phosphorus-Use Efficiency

Fast-growing annuals, including annual crops, are characterised by rapid photosynthetic rates (mass based), high leaf P concentrations, and low leaf mass per area (LMA). These characteristics are associated with a high **photosynthetic P-use efficiency** (photosynthesis rate per unit leaf phosphorus, PPUE) [35,36]. Moreover, PPUE can vary by an order of magnitude at any LMA, and part of this variation is associated with leaf N concentration. For crops grown in low-P soils (high N:P ratio), a high PPUE is expected [37]. The factors determining variation in PPUE among and within crop species are largely not known, and warrant further studies, building on what we know from wild species [38].

In crop canopies, only some leaves operate at full photosynthetic capacity, and only for part of the day. Cereals with mostly erect leaf orientations would maintain rapid photosynthetic rates across leaf layers and, thus, maintain higher PPUE throughout the canopy. However, as the light penetration to lower leaf layers becomes marginal for broad-leaf crops, PPUE at lower leaf layers declines rapidly. Therefore, rapid retranslocation of P from lower leaf layers before senescence is important in broad-leaved crops. Interestingly, leaf inclination in rice is regulated by P signalling, illustrating how P can modulate crop canopy for efficient photosynthesis [39]. Thus, it is necessary to explore the natural variation of crops in P metabolism and signalling, and identify and examine those cultivars with efficient PPUE in agricultural fields.

Rapid rates of photosynthesis and high PPUE require a fine balance between P allocation to different leaf cell types and P pools [40,41]. At the leaf level, P is preferentially allocated to photosynthetic cells in monocots [42], and eudicots that evolved in P-limited landscapes [43,44]. At the cellular level, replacement of **phospholipids** by sulfolipids and galactolipids [45,46], and functioning at very low levels of **ribosomal RNA** [47] are associated with a high PPUE. The PPUE is positively correlated with the ratio of metabolic P to lipid P (i.e., a greater investment of P in P-containing metabolites for maintaining photosynthesis and a smaller investment in phospholipids) [46]. Understanding the mechanisms involved in preferential P allocation to different leaf cell types and different P fractions is important when aiming to develop crop species or cultivars with high PPUE. This P-allocation pattern may have significant implications for increasing crop yield or reducing P-fertiliser input.

Phosphorus-Remobilisation Efficiency

Adequate P nutrition is important to ensure high biomass production and partitioning of biomass to grain over leaves and culms during the heading and maturity stages. Plants remobilise internal P, and this is important when soil P supply is limited.

Remobilisation of internal P is **facilitated** by transporting P from old organs to young and/or actively growing ones [48]. This is preceded by the breakdown of plasma-membrane components [49], and replacement of membrane phospholipids by lipids that do not contain P. Moreover, ribonuclease activity is increased [50], leading to hydrolysis of RNA, and smaller P esters are broken down [51]. Understanding cellular processes enhancing P remobilisation and the influence of external factors on these processes is vital in developing crop-improvement programs.

Senescing leaves act as a source for grain P in cereals; for example, 10–70% of absorbed P can be mobilised from older to younger leaves and grains in wheat (*Triticum aestivum*), maize and rice, depending on P nutrition, growth stage and management [52–55]. In rice, when a green leaf P concentration is in the range of 1500–2500 $\mu\text{g g}^{-1}$, senescing leaf P concentrations may decline to <500 $\mu\text{g g}^{-1}$ due to remobilisation. Straw P concentrations of 600 $\mu\text{g g}^{-1}$ and grain P concentrations of 1600 $\mu\text{g g}^{-1}$ are generally considered as deficiency thresholds in rice [56]. In maize,

Ribosomal RNA: RNA component of ribosomes, the protein-synthesising machinery in cells.

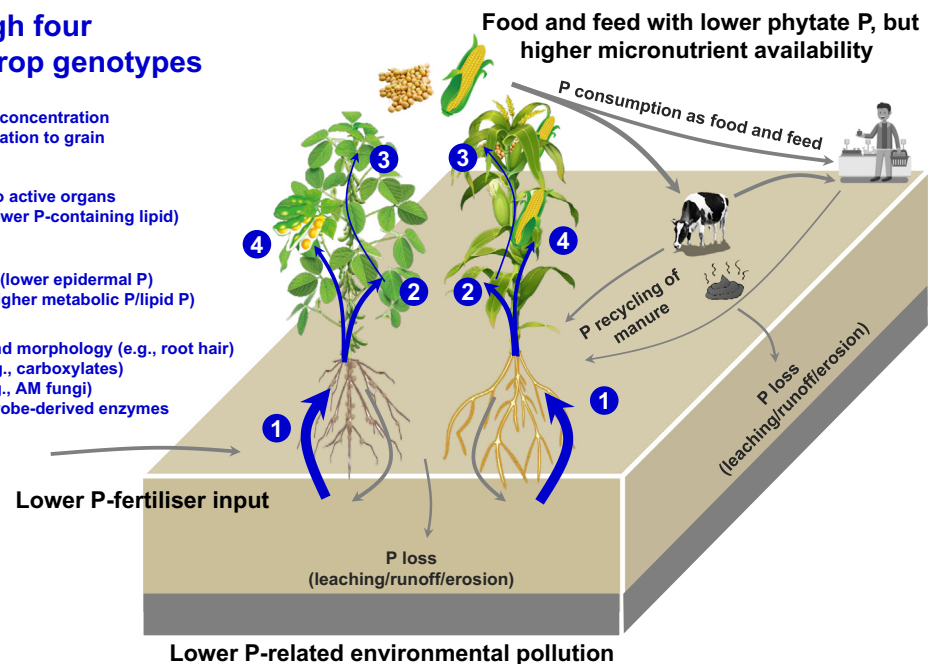
Rock phosphate: the raw material used in manufacturing phosphate fertiliser. It is a nonrenewable, finite, and dwindling natural resource; hence its use requires our best stewardship.

Key Figure

Tightening the Phosphorus (P) Cycle through P-Efficient Crop Genotypes

Tightening P cycle through four strategies of P-efficient crop genotypes

- 4 **Seed P (phytate) concentration**
 - Low phytate P concentration
 - Low P translocation to grain
- 3 **P-remobilisation efficiency**
 - High transfer to active organs
 - Cell P pools (lower P-containing lipid)
- 2 **Photosynthetic P-use efficiency**
 - Leaf cell types (lower epidermal P)
 - Cell P pools (higher metabolic P/lipid P)
- 1 **P-acquisition efficiency**
 - Architecture and morphology (e.g., root hair)
 - Physiology (e.g., carboxylates)
 - Symbioses (e.g., AM fungi)
 - Plant- and microbe-derived enzymes



Trends in Plant Science

Figure 1. We propose four strategies to explore genetic variation in cereals and grain legumes to enhance the efficiency of P acquisition, utilisation, and remobilisation, and to reduce seed total P and phytate P concentrations in crop production systems (blue). These strategies will have implications for the P cycle in animal production and human consumption systems (gray), leading to reduced P-fertiliser requirement, enhanced nutritional quality of food and feed, and decreased P-related environmental pollution (black). Abbreviation: AM, arbuscular mycorrhizal.

regardless of P-application rates, P remobilisation to the ear during the first half of the grain-filling phase is primarily from the stem (50–76%), rather than from the leaves (30–44%) [55]. However, senescing leaves act as the key source of P for maize grains towards the end of the grain-filling phase. Some native plants decrease their leaf P concentrations much further than cereal do (i.e., to 27–196 $\mu\text{g g}^{-1}$) [57]. These very low values are only partly accounted for by their higher LMA.

Crop cultivars show high genetic variability for P-deficiency tolerance [51,54,58,59]. When comparing P-deficiency-tolerant and susceptible rice cultivars, P-deficiency-tolerant rice cultivars grown under P-deficient conditions have remarkably lower P concentrations in less active vegetative organs (partly and fully senesced leaves) compared with those of susceptible rice cultivars; conversely, more active organs (green leaves and panicles) contain a greater concentration of P [51,53,54]. This greater plasticity of tolerant cultivars to external P availability can be a genetic resource for developing low-P-tolerant, high-yielding rice cultivars suitable for P-limited environments.

Variation in Seed Total and Phytate Phosphorus Concentration

Phytate, a mixture of salts of phytic acid, is a storage form of P, especially in seeds, typically representing >75% of seed total P [60]. A high seed phytate concentration is not a desirable trait, because phytate renders zinc and other micronutrients unavailable for humans and

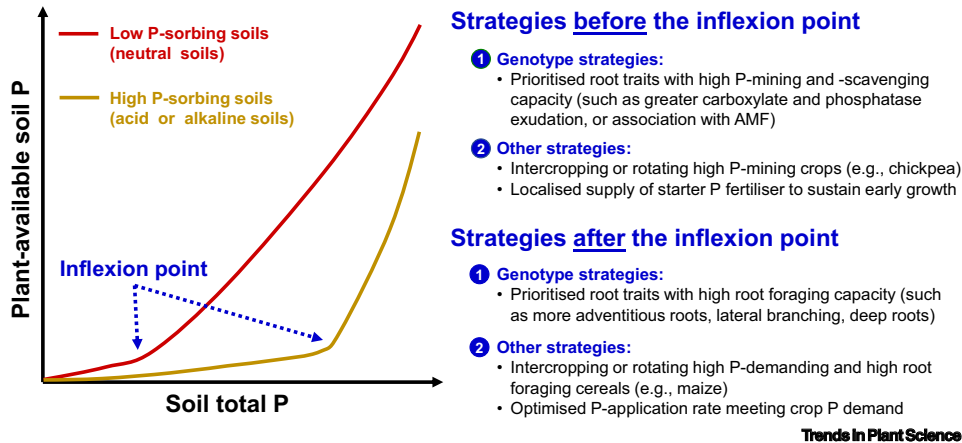


Figure 2. Efficient Phosphorus (P)-Acquisition Strategies Strategies for Different Soil Types and Soil P Status. Genotype strategies related to soil P acquisition and other agricultural strategies (diversified cropping system and P-fertiliser management) are recommended for high and low P-sorbing soils. Abbreviation: AMF, arbuscular mycorrhizal fungi.

livestock, contributing to malnutrition (e.g., iron and zinc deficiency), especially for children in developing countries [61]. In addition, phytate cannot be efficiently utilised by humans and non-ruminant animals (e.g., pigs), contributing to high losses of P to the environment.

So far, there have been three main approaches to reduce phytate concentrations to mitigate its negative impacts. First, classical and/or molecular techniques have been used to disrupt phytate synthesis during seed development, leading to a decreased phytate P proportion of seed total P [61]. Second, molecular techniques can also be used to reduce P transport to seed. For example, knockout of a gene (*SPDT*) in rice does not affect grain yield, but significantly decreases P allocation to the grain, reducing P removal from the field and subsequent potential P-related environmental risk [62]. Yet, the genetically modified approach may have potential adverse effects on environment and health. Finally, classical variety trials have been used to select for low phytate P concentrations.

We reviewed the literature for the main grain cereals and legumes, investigating the variation in seed total P and phytate P concentrations across genotypes (Figure 3). Soybean (*Glycine max*) exhibits the highest seed total P and phytate P concentration among all crops, whereas chickpea shows the lowest seed phytate P concentration. Moreover, variation in seed phytate P concentration is also greatest in soybean (1.7–13.3 mg g⁻¹), indicating the potential in identifying genotypes with low phytate concentration. In addition, assessing 274 soybean genotypes showed that genotypes with lower seed total P concentrations have higher grain yield [63]. Pea (*Pisum sativum*) is a low-P-demanding crop compared with soybean and peanut (*Arachis hypogaea*), suggesting the potential for reducing P fertiliser input, but there are few data on phytate available for pea [64,65]. Modern wheat cultivars generally have higher phytate concentrations compared with older cultivars [66]. Therefore, modern breeding should consider not only high yields, but also low phytate concentrations. Concerns have been raised that lower seed total P concentration may negatively influence seedling growth, but these concerns are not supported by recent studies showing that seedling growth of rice was unaffected by seed total P concentration [67–69].

Integrating Crop Genotype and Other Agronomic Strategies to Tighten the Phosphorus Cycle

Can we integrate all four strategies targeting crop genotypes and prioritise the strategies in case of trade-offs between them to tighten the P cycle for agriculture with different soil P status? We

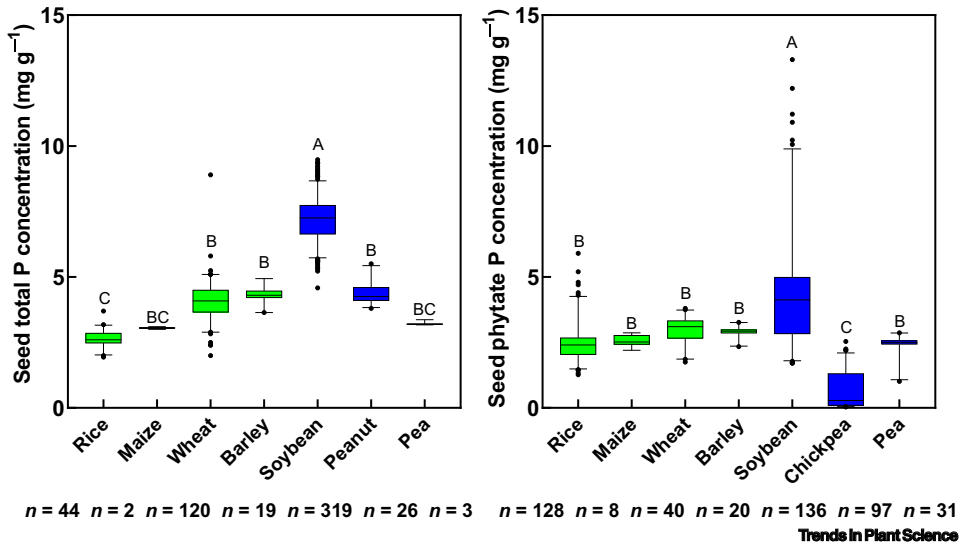


Figure 3. Box Plots of Seed Total Phosphorus (P) and Phytate P Concentrations in Cereals (Green Boxes) and Grain Legumes (Blue Boxes). Rice (*Oryza sativa*): [74–76]; maize (*Zea mays*): [77,78]; wheat (*Triticum aestivum*): [66,79,80]; barley (*Hordeum vulgare*): [79,81]; soybean (*Glycine max*): [63,74,79,82–86]; peanut (*Arachis hypogaea*): [87]; chickpea (*Cicer arietinum*): [88,89]; and pea (*Pisum sativum*): [64,65]. Means with different capital letters are significantly different ($P < 0.05$) using Tukey's *post hoc* test. Note that certain data points of phytate P concentration exceeded the seed total P concentration because some papers do not report seed total P concentrations.

classified soils into four types with high/low soil total P or plant-available soil P, and recommend prioritised genotype strategies for each soil type according to their relative importance (Figure 4). Among all four strategies, lower seed phytate concentration and higher P-acquisition efficiency

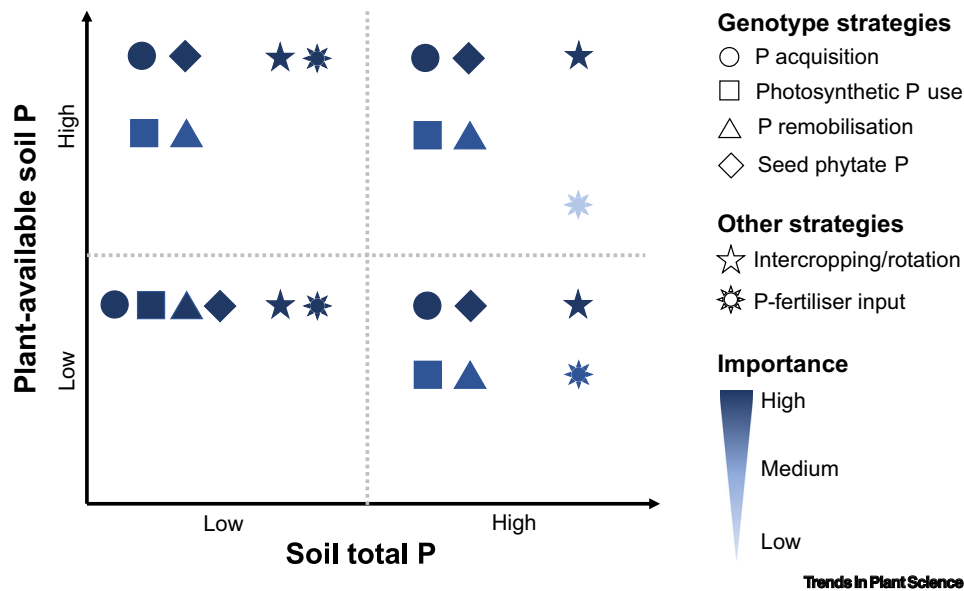


Figure 4. Strategies to Tighten the Phosphorus (P) Cycle in Agriculture for Soils with Different P Status. Soils are classified into four types: low total P and plant-available P (bottom left), low total P, but high plant-available P (top left), high total P, but low plant-available P (bottom right), and high total P and plant-available P (top right). We recommend different strategies comprising crop genotypes, cropping systems, and P-fertiliser input for each soil type to tighten the P cycle, while sustainably maintaining crop production.

are important in all soil types. Lower seed phytate concentration is crucial for soils with high plant-available P in many areas of China and Western Europe containing substantial amounts of residual soil P [34], because it can substantially save P-fertiliser input, reduce P-related environmental impacts as well as enhance micronutrient availability of food and fodder [61]. This advantage concerning crop nutrition is also relevant to soils with low plant-available P concentration, such as in some countries of Africa, where hidden hunger is a crucial issue. High P-acquisition strategies have a key role in soils with high plant-available P through strong root foraging capacity, while they are also desirable for soils with lower available P via high P-mining capacity. Strategies related to PPUE and P-remobilisation efficiency have an equally important role as P acquisition and seed phytate concentrations in low total P and plant-available P soils in enhancing P-use efficiency.

Genotype strategies could be combined with agronomic strategies to jointly enhance P-use efficiency (Figure 4). Diversified cropping systems, such as intercropping or rotations, can effectively enhance P-use efficiency by including targeted crop species or varieties characterised by high P-mobilising or P-uptake capacity dependent on soil P status. Moreover, P-fertiliser input is a desirable agronomic practice to enhance plant growth, especially in P-impoverished soils [70]. In addition, starter-P fertiliser is an efficient way to boost early plant growth through stimulating root growth. P-fertiliser input is also important in sandy soils with a low P-buffering capacity to grow P-demanding crops [71]. Overall, integrating strategies of appropriate crop genotypes with corresponding agronomic strategies will help tighten the P cycle.

Concluding Remarks and Perspectives

Tightening the P cycle through P-efficient genotypes is a promising way for simultaneously conserving nonrenewable P resources, enhancing food nutritional quality, and mitigating negative environmental impacts. To achieve this, we should judiciously consider combining crop genotypes varying in P-acquisition, -utilisation, -remobilisation efficiency, and low seed phytate P concentration with agricultural management practices, such as diversified cropping systems and P-fertiliser application, for a given environmental context. In addition to P acquisition, we show a large variation in seed phytate P concentration of common cereals and grain legumes, indicating that crop genotypes have the potential to reduce P-fertiliser use and enhance the micronutrient availability of food and fodder. Yet, the variations in PPUE and P-remobilisation efficiency among and within crop species and the driving factors are largely unknown, and warrant further studies. Moreover, to better understand the potential roles and underlying mechanisms of crop genotypes in tightening the P cycle of cropping systems, future work could examine the effect of straw and/or root residues of crop genotypes on subsequent crops and reveal the underlying mechanisms [72]. Future work may extend current perspectives around tightening the P cycle from cropping systems to whole agrifood systems, including animal production, food processing, and human consumption [73]. This could help understand the importance of P-efficient crop genotypes in terms of environmental impacts and the profitability of different stakeholders from the food-chain perspective (see also Outstanding Questions).

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Outstanding Questions

Is there an easily measurable proxy to detect root-associated-microbe P acquisition, such as leaf [Mn] for rhizosphere carboxylates and blumenols for mycorrhizal colonisation?

Which crop species mixtures synergistically enhance plant P acquisition?

Which factors determine the variation in P-use efficiency among and within crop species?

Is there an optimised proportion of P allocation to different leaf cell types and P fractions for high photosynthetic P-use efficiency?

Which cellular processes determine P-remobilisation efficiency, and how do external factors (e.g., soil P-sorption capacity) influence these processes?

To what extent can P-efficient crop genotypes contribute to reduce P-related environmental impacts and improve nutrition in the entire agrifood systems?

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