

REVIEW

# Phosphorus use efficiency and fertilizers: future opportunities for improvements

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**Abstract** The continued supply of phosphate fertilizers that underpin global food production is an imminent crisis. The rock phosphate deposits on which the world depends are not only finite, but some are contaminated, and many are located in geopolitically unstable areas, meaning that fundamental changes will have to take place in order to maintain food production for a growing global population. No single solution exists, but a combination of approaches to phosphorus management is required not only to extend the lifespan of the remaining non-renewable rock phosphate reserves, but to result in a more efficient, sustainable phosphorus cycle. Solutions include improving the efficiency of fertilizer applications to agricultural land, alongside a better understanding of phosphorus cycling in soil-plant systems, and the interactions between soil physics, chemistry and biology, coupled with plant traits. Opportunities exist for the development of plants that can access different forms of soil phosphorus (e.g., organic phosphorus) and that use internal phosphorus more efficiently. The development of different sources of phosphorus fertilizers are inevitably required given the finite nature of the rock phosphate supplies. Clear opportunities exist, and it is now important that a concerted effort to make advances in phosphorus use efficiency is prioritized.

**Keywords** organic phosphorus, phosphorus fertilizer, phosphorus use efficiency, rock phosphate

## 1 Introduction

The commercial inorganic phosphorus fertilizer industry began in 1842 when Sir John Bennett Lawes of Rothamsted Research, UK, patented the first commercial phosphate fertilizer, or “chemical manure”. Lawes created

his fertilizer by dissolving animal bones in sulfuric acid, creating what was termed “superphosphate”. While proving a great success, there were not enough bones to supply the increasing demand for phosphorus fertilizers and alternative sources of phosphorus were sought and the rock phosphate industry was developed. Today, global food production is highly dependent upon phosphorus fertilizers produced from the processing of rock phosphate, although these deposits occur in a limited number of locations globally.

The largest rock phosphate deposits occur in Morocco and Western Sahara with an estimated 50 Gt of rock phosphate available, while China, having the second largest known reserves of about 3.3 Gt mines the largest quantities of rock phosphate<sup>[1]</sup>. Table 1 shows the estimated rock phosphate reserves and recent rates of production of some of the key countries from which phosphate is sourced. Although the overall estimate of 259 years of rock phosphate remaining at current production rates suggests there are no imminent issues regarding phosphate supplies, if trends in mining and geopolitical considerations are considered, some interesting statistics arise. For example, this global estimate of 259 years of future supply was reduced from about 300 years just 3 years ago, reflecting increasing demand. China holds the second largest reserves in the world and is the greatest producer of rock phosphate (with no exports), but has only 24 years of supply remaining at current production rates, while India and the USA have only 29 and 37 years of supply, respectively. If the estimated remaining number of years supply of rock phosphate continues to decline at the current rate (i.e., 300–259 years of supply in 3 years, a 14% change in the estimate), it could be argued that all supplies will be exhausted by 2040. While this latter scenario is unlikely, it does highlight that significant changes in demand are occurring and that imminent, fundamental changes in the global phosphorus trade, use and recycling efforts will be necessary in order to secure phosphorus availability. This is especially pertinent in China, India and the USA, the three countries with largest populations on

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**Table 1** World mine production of rock phosphate and current known reserves in thousand tonnes

| Country                    | Mine production in 2018/kt | Current reserves/kt | Years of reserves remaining |
|----------------------------|----------------------------|---------------------|-----------------------------|
| China                      | 140000                     | 3200000             | 23                          |
| India                      | 1600                       | 46000               | 29                          |
| United States              | 27000                      | 1000000             | 37                          |
| Algeria                    | 1300                       | 2200000             | 1692                        |
| Australia                  | 3000                       | 1100000             | 367                         |
| Brazil                     | 5400                       | 1700000             | 315                         |
| Egypt                      | 4600                       | 1300000             | 283                         |
| Finland                    | 1000                       | 1000000             | 1000                        |
| Israel                     | 3900                       | 67000               | 17                          |
| Jordan                     | 8800                       | 1000000             | 114                         |
| Kazakhstan                 | 1600                       | 260000              | 163                         |
| Mexico                     | 2000                       | 30000               | 15                          |
| Morocco and Western Sahara | 33000                      | 50000000            | 1515                        |
| Peru                       | 3100                       | 400000              | 129                         |
| Russia                     | 13000                      | 600000              | 46                          |
| Saudi Arabia               | 5200                       | 1400000             | 269                         |
| Senegal                    | 1500                       | 50000               | 33                          |
| South Africa               | 2100                       | 1500000             | 714                         |
| Syria                      | 100                        | 1800000             | 18000                       |
| Togo                       | 850                        | 30000               | 35                          |
| Tunisia                    | 3300                       | 100000              | 30                          |
| Uzbekistan                 | 900                        | 100000              | 111                         |
| Vietnam                    | 3300                       | 30000               | 9                           |
| Other countries            | 1300                       | 770000              | 592                         |
| World total (rounded)      | 270000                     | 70000000            | 259                         |

Note: Years of reserves remaining are calculated by dividing known reserves by the latest annual rate of mine production<sup>[1]</sup>.

the planet, which rely on rock phosphate to feed their people. Another threat to the supply of phosphate fertilizer is that countries with some of the largest deposits, e.g., Algeria, Jordan and Syria are situated in areas of recent political instability, meaning rock phosphate deposits do not necessarily need to become depleted before the effects of scarcity on food production are noticed. It is important to recognize that these statistics oversimplify a much more complex issue of phosphate fertilizer supply, global reserves and trade dynamics, as presented by Cordell and White<sup>[2]</sup>. However, there is generally a consensus among researchers that phosphorus fertilizer supply is a crucial aspect of future global food security. Therefore, in the face of this potential crisis in availability of rock phosphate in key parts of the world, there is a pressing need to look again at how phosphate fertilizer is used, where it can be obtained, how it can be most efficiently used in agriculture, and potential alternative sources for the production of phosphate fertilizer.

## 2 Improving phosphorus use efficiency: what are the problems?

Phosphate cycling in soils is extremely complex, being controlled by a range of different physical, chemical and biological factors. In combination, this means it is difficult to accurately determine the quantity of phosphate fertilizers required for optimal crop growth in different types of soils. Depending on the soil type, its existing physical condition and chemical status, it is estimated that no more than 8% of phosphorus added to soil in fertilizers is recovered in crops<sup>[3]</sup>. The remainder is either adsorbed to different degrees to soil particles and organic matter, taken up by soil microbes, organically complexed or lost to surface waters. Historically, to ensure optimum yields it became commonplace for farmers to adopt a prophylactic approach to the use of phosphorus fertilizers involving over-application. This has led to an accumulation of phosphorus in soils in forms that are often described as

slowly available phosphorus. This accumulation brings with it another set of problems, because it is vulnerable to both leaching and loss by erosion, resulting in eutrophication of surface waters<sup>[4]</sup> and also represents a significant inefficiency in phosphorus use. However, it also now represents a reserve of phosphorus that can potentially be exploited for agricultural production<sup>[5–7]</sup>, if the correct technology and management interventions are developed and utilized, as described below.

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### 3 How much phosphorus fertilizer do crops require?

One of the most important factors in ensuring phosphorus fertilizer use efficiency is in the calculation of the amount required to be added to soils for optimum plant growth. The usual process for determining how much phosphorus is required to be added is a two-stage process. First, the measurement of the available phosphorus status of the soil. Then, using tables derived from critical-phosphorus experiments (see Section 5), recommendations on the quantity of phosphorus required to be added to the soil for specific crops can be made. There are many potential problems with this process, not least the fact that the different adsorption properties of different soil types are seldom taken into consideration although some systems do account for soil type, e.g., the recommendations of Scotland's Rural College for managing soil phosphorus<sup>[8]</sup>. Also, often the method of measurement of available phosphorus is inaccurate and not appropriate for the soil type, i.e., whether it is in an acidic or alkaline soil.

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### 4 Measuring soil available phosphorus

In Europe alone, there are more than ten different soil tests used as standard measurements of available soil phosphorus<sup>[9]</sup>. These standard tests typically involve extraction of soils with solutions that either decrease the soil-solution ratio, impose a pH change or add anions that displace phosphate ions from soil surfaces. The result is the measurement of phosphorus in the soil solution and from pools that were relatively loosely adsorbed to the soil, with such approaches referred to as phosphorus quantity tests. The concentration of inorganic reactive phosphorus in the extractant is then measured using standard analytical techniques. Recently, interest has grown in the use of sink methods, some of which were developed quite a long time ago, such as resin strips<sup>[10]</sup> or diffusive gradients in thin films (DGT)<sup>[11]</sup>. These are purported to more realistically represent the action of a plant root than simple solution extraction techniques as they remove phosphorus from the soil solution, thus stimulating the resupply of soil-solution phosphorus and better reflect true phosphorus availability. These methods are referred to as phosphorus

intensity tests. Whichever type of test is used, ultimately it is the relationship between the value measured at the start of a crop cycle (or growing season) to the growth response of plants that is important, and the better that relationship, the more useful the soil test. Another important measurement when determining availability of phosphorus and how much fertilizer needs to be added is the phosphate buffer index (PBI) or capacity (PBC) of a soil. This is a measure of the ease with which phosphorus associated with the solid soil fraction can become soluble, or conversely the capacity of a soil to lock up added phosphorus, making it unavailable for plant uptake. Soils with a high PBI generally require high application rates of phosphorus fertilizer to achieve target available phosphorus indices<sup>[12]</sup>. The issue is further complicated by the fact that adding the same amount of phosphorus fertilizer to different soils that have the same available phosphorus quantity or intensity values does not necessarily result in the same final available phosphorus value. This is because PBI is affected by differences in soil physical, chemical and biological properties and phosphorus can be adsorbed or fixed in different ways and can subsequently have different desorption kinetics. This metric of the capacity of soil to adsorb phosphorus from phosphorus added in fertilizers, and buffer phosphorus in the soil solution, is increasingly recognized as important. Consequently, it is now incorporated in some recommendation systems alongside measurements of available phosphorus to help better predict the fertilizer requirements of different soil/crop systems, e.g., the Morgan soil test in Scotland<sup>[8]</sup>.

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### 5 Critical-phosphorus tests

To determine whether a soil should receive phosphorus fertilizer applications, the available phosphorus determined by the soil extraction is compared to predetermined target index values. In the UK, the most commonly used measure of available phosphorus involves an Olsen (sodium bicarbonate) extraction, and currently target phosphorus values are generally recommended as 16–25 mg·L<sup>-1</sup> P in soil (referred to as Index 2); at or below these values, phosphorus applications are advised that maintain or raise soil available phosphorus concentrations to levels that are assumed to be optimal for plant growth<sup>[13]</sup>. These target levels are not determined according to the specific soil and crop but are derived from historical critical-phosphorus tests. In these tests, crop yield is measured in a single soil at increasing soil phosphorus concentrations, and a typical example is given in Fig. 1, with barley grain biomass grown in a low-phosphorus, organic soil<sup>[14]</sup>. Characteristically, for a critical-phosphorus curve yield increases with phosphorus additions, but eventually plateaus when phosphorus is no longer the yield-limiting factor. The shape of the response indicates that phosphorus additions bring diminishing returns, and in

Fig. 1, 90% of the maximum yield is attained by adding  $464 \pm 77.9 \text{ mg} \cdot \text{kg}^{-1} \text{ P}$  in soil (about  $557 \text{ kg} \cdot \text{ha}^{-1} \text{ P}$ ). This quantity may seem high, but it should be remembered that the initial available phosphorus (Olsen phosphorus) value of the soil was  $6.7 \text{ mg} \cdot \text{L}^{-1} \text{ P}$ , and that earlier it was explained that typically less than 8% of the added phosphorus is recovered in the crop. Changing the phosphorus status of an Index 0 soil to that of optimum available phosphorus concentration initially requires considerable inputs and increases in soils with higher PBI. In Fig. 1, 95% of the maximum yield is achieved at  $600 \pm 103 \text{ mg} \cdot \text{kg}^{-1} \text{ P}$  in soil (about  $720 \text{ kg} \cdot \text{ha}^{-1} \text{ P}$ ), further demonstrating that as the soil phosphorus status increases, a modest increase in yield requires considerable additional phosphorus fertilizer. Thus, farmers have to make decisions on what available phosphorus value to target in relation to potential profit.

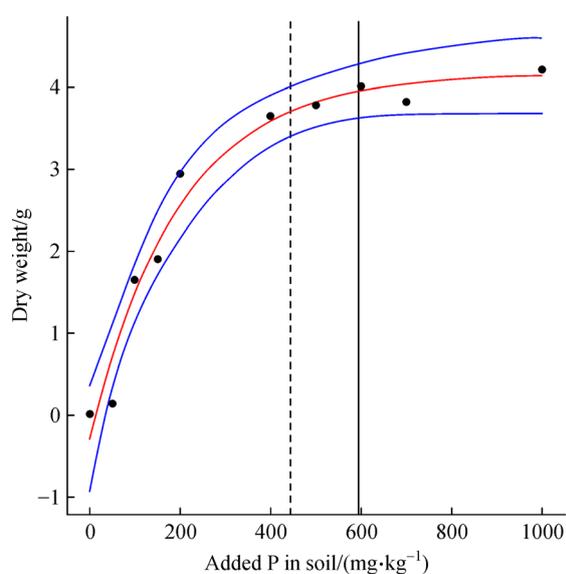


Fig. 1 Response of barley grain biomass to soil phosphorus additions. Curved lines are the best fit at 95% confidence intervals. The dashed and solid vertical lines represent the phosphorus additions required to achieve 90% and 95% of the maximum yield, respectively.

Most soil phosphorus tests do not enable the consideration of the plant contribution to phosphorus availability, e.g., via the production of organic acids and phosphatase enzymes respectively, which affect the adsorption and forms (via mineralization) of phosphorus in soils. Continuous cycling of phosphorus through organic and inorganic forms by soil microbes further complicate the situation and in combination all these factors mean that the available phosphorus status of a soil is continually changing. These complexities mean that soil tests are not applicable universally to all soil types, although many researchers have tried to find such a test. For example,

Nawara et al.<sup>[15]</sup> examined the ability of five different soil tests (three quantity and two intensity tests) to predict yields from 11 soil types from long-term experiments in Europe and found that no test was superior to any another for predicting critical-phosphorus values across the range of soil types. In soils with high PBC, the performance of intensity tests, such as the DGT, has been shown to predict plant growth more accurately than other soil phosphorus tests<sup>[16,17]</sup>. This supports the argument that, rather than continuing to use single soil tests across a range of soil types, the range of soil types to which individual soil tests can be applied requires refining.

Further improvements in the prediction of critical-phosphorus values can be achieved through modification of the extraction methods, as demonstrated in recent work by Recena et al.<sup>[18]</sup>. Their study supports the case for developing different phosphorus fertilizer recommendations for different soil types, as well consideration of the role of organic phosphorus in plant nutrition. Regarding the former, they found that variance in cumulative phosphorus uptake explained by Olsen extractable reactive phosphorus in 36 soils used in a phosphorus depletion experiment increased from 47%, when all soils were considered together, to 63%, when soils were separated into two groups based on their calcium-carbonate equivalent to clay ratio. Measuring total phosphorus instead of just reactive phosphorus increased the value to 59% when considering all samples, but when separated into the two groups, this further increased to 73%. It is reported that most of the additional phosphorus measured when total phosphorus is measured in extracts compared to reactive phosphorus is usually in organic form. The findings by Recena et al.<sup>[18,19]</sup>, that considering total phosphorus in Olsen extracts gives a better relationship with yield than measurement of reactive phosphorus alone, indicates that organic phosphorus does contribute to plant nutrition and needs to be considered when making fertilizer recommendations.

Although organic phosphorus was previously considered unavailable to plants, work by George et al.<sup>[20]</sup> and Giles et al.<sup>[21]</sup>, among others, has shown that plants can be engineered to use soil organic phosphorus by increasing their production of root exudates such as organic acids and phosphatase enzymes. Organic phosphorus commonly constitutes 30%–90% of the total phosphorus in soils<sup>[6]</sup>. More efficient utilization of this soil resource would help improve crop yields and phosphorus use efficiency in agricultural systems where access to fertilizers is limited. For example, it is estimated there is enough monoester phosphorus in soils globally to provide average crop nutrition for about 117 years<sup>[7]</sup>. Microorganisms are also known to contribute to the mobilisation and hydrolysis of soil organic phosphorus for uptake by plants, but the nature of the relationships and relative roles of plants versus microbes are still largely unknown.

## 6 A change in philosophy

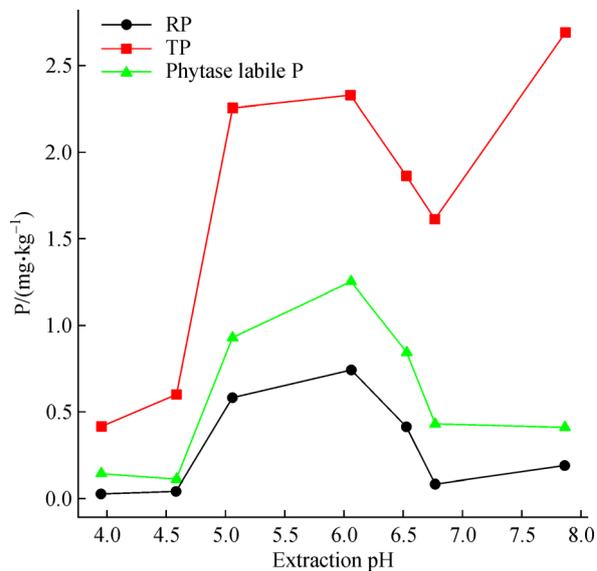
A 10-year research program into phosphorus management in arable crops by the Agriculture and Horticulture Development Board, UK, recently published its findings<sup>[3]</sup>. One of the key recommendations was a move toward a fundamental change in approach for phosphorus fertilization based on the philosophy of “feed the crop, not the soil”<sup>[22]</sup>. This incorporates allowing soil phosphorus index to fall below the conventional recommendation of Index 2 (16–25 mg·L<sup>-1</sup> P)<sup>[3]</sup> to Index 1 (10–15 mg·L<sup>-1</sup> P) in some situations, especially if soil structure is suitable. Subsequent applications of phosphorus then reflect crop requirements, not higher soil phosphorus requirements. Such an approach requires regular testing of soils for available phosphorus to ensure this lower phosphorus status is not reduced, but is maintained at the required level, as potentially there is less room for error in the sometimes-unreliable existing soil tests. Other recommendations include the measurement of grain phosphorus as an indicator of phosphorus deficiency, and incorporation of other measures of phosphorus availability in soils, e.g., PBI (see above).

Given these increases in understanding, there are two approaches that can be proposed for the improvement of soil testing in order to make better phosphorus application rate recommendations. (1) Redesign soil tests to use extractants that are appropriate, e.g., reflect what is happening in the root zone (organic acids) and utilize them for specific soil types and crop types. (2) Develop a more dynamic method of understanding and considering the phosphorus requirements of plants, considering both organic and inorganic phosphorus availability to plants, and universal incorporation of important metrics such as PBI. Achieving these aims will require considerable investment in a long-term program of practical field and laboratory studies that accounts for soil, crop, fertilizer and climatic variability along with different soil tests. These need to be accompanied by the development of faster, simpler and more reliable field tests for measuring soil phosphorus status, to enable farmers themselves to carry out frequent testing, rather than relying on sending samples to laboratories.

## 7 Soil pH

There has been extensive research into the value of maintaining soil pH at optimum values to maximise the availability of reactive phosphorus, with a pH of between 6 and 6.5 generally being considered appropriate for most soils<sup>[23]</sup>. Another window of availability occurs at around pH 4.5, but despite this being suitable for the availability of phosphorus, it is too acidic for the growth of most crops. However, there has been little research into the effect of pH

on the mobility or bioavailability of organic phosphorus compounds. With regard to soil organic phosphorus, Turner and Blackwell<sup>[24]</sup> reported that, except under strongly acidic conditions, pH had little impact on the abundance of different forms of organic phosphorus in arable soil that had not received any phosphorus inputs for more than 160 years. However, of more relevance to agriculture today, organic phosphorus can comprise a significant proportion of the total phosphorus in organic fertilizers, such as livestock manure and slurry. In a meta-analysis, Darch et al.<sup>[25]</sup> found organic phosphorus to comprise about a quarter of the total extractable phosphorus in these fertilizers. Furthermore, a proportion of the organic phosphorus may be easily hydrolysed to phosphate once it is in soil solution<sup>[25]</sup>. Consequently, it is important to understand the effect of pH on the mobility of organic phosphorus, and the results for a single soil are shown in Fig. 2. An acidic soil with an initial pH of 5.1 was adjusted to a range of soil pH between 4 and 8. It was then extracted with ultrapure water and analyzed for reactive, total and phytase-labile phosphorus. The data indicated that total phosphorus extraction was greatest at moderately acidic pH, pH 5–6, although it appeared to increase again at pH 7.8 (Fig. 2). The trend of reactive phosphorus and phytase labile phosphorus concentrations also followed this same pattern, with the exception of a further increase at alkaline pH. The proportion of the total phosphorus that is phytase-labile changed with pH, from 30% at pH 4.5 and 7.5, to 90% at pH 6 (Fig. 2). This implies that by maintaining (acidic) soils at pH 5–6, the availability of the phosphorus applied in fertilizer, or that which is already contained in soil, is maximized, meaning that requirements



**Fig. 2** Effect of pH on the concentration of total phosphorus (TP), reactive phosphorus (RP), and phytase labile P extracted in ultrapure water.

for additional phosphorus fertilizers will be reduced. However, the lack of data on the effect of pH on organic phosphorus availability across a range of soil types and phosphorus contents means that pH recommendations differ according to the proportion of soil phosphorus that is in an organic form.

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## 8 Micronutrient antagonism and synergism

Another topic that is poorly understood but may impact on phosphorus availability and uptake by plants is related to the interactive effects of phosphorus and different micronutrients and toxic trace elements, including Cd (Nino-Savala et al.<sup>[26]</sup>). No interaction between any two nutrients added to the soil from a fertilizer is possible, such that the yield response to the nutrients is the sum of the response to the two nutrients added individually<sup>[27]</sup>. However, there may also be synergistic or antagonistic interactions between the nutrients, such that the yield response is either larger or smaller than expected from the effect of the individual nutrients<sup>[27]</sup>. Synergistic effects have been reported between phosphorus and N, Mg, Mn and Mo, but excess soil phosphorus has been shown to induce deficiencies of nutrients including S, K, Fe, Cu, Zn and Fe<sup>[28,29]</sup>. It is sometimes unclear if these antagonistic effects result in decreased concentrations of nutrients in crops, or reduced yields, or both, but both are important for food security<sup>[30]</sup>. Potential reasons for the antagonistic effects of phosphorus on other nutrients are varied, but can include phosphorus affecting the mobility of other elements in the soil, affecting the uptake, translocation or utilization of the other nutrients, or dilution of them in the plant material due to an increase in dry matter production<sup>[29]</sup>. However, it is clear that the interactions between elements are complex, and can vary between studies<sup>[27]</sup>, possibly due to soil or plant differences, or variation in the ratios of different nutrients. Despite the importance of plant nutrient interactions for determining the efficiency of use of nutrients applied to soil in fertilizers, this topic has received relatively little attention. However, without this information it will not be possible to design future sustainable agricultural systems, especially with the increasing prevalence of precision agriculture, therefore further research is imperative.

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## 9 Novel fertilizers

Opportunities also exist through the development of novel types of fertilizers, which may have different phosphorus solubility or release kinetics, based on their physical and chemical properties. This may arise due to the sourcing of phosphorus fertilizers from materials other than rock phosphate. This is something that is not only an opportunity but also an imperative, given the issues

surrounding the continued supply of phosphate fertilizers derived from rock phosphate deposits, as discussed earlier. Recycled phosphorus fertilizers will undoubtedly increase in prevalence in the coming years, providing considerable opportunities for innovation, for example, in their formulation and release kinetics. Examples of recycled fertilizers include struvite-based fertilizers recovered from sewage works, calcium phosphate from the demineralization of milk products from the dairy industry and processed abattoir wastes that are rich in phosphate from bones.

As well as managing the soil, there are many opportunities to improve phosphorus fertilizer use efficiency by influencing different plant traits, as discussed above in relation to plant root exudates. Root morphology is one such example and has received considerable attention<sup>[31]</sup>, but other opportunities exist with the development of plants with the capacity for active in planta phosphorus management and apportionment.

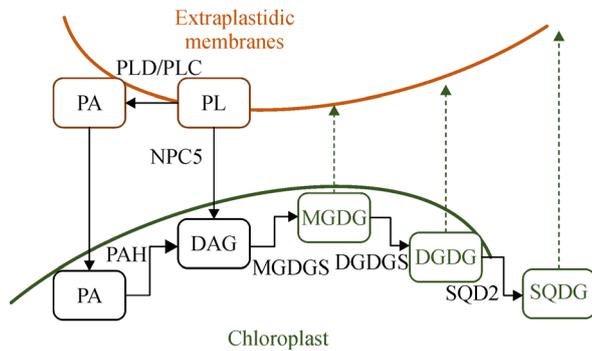
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## 10 Membrane lipid remodeling: a strategy to improve crop phosphorus use efficiency

Phosphate forms a major component of fundamental biomolecules such as nucleic acids, adenosine phosphates and phospholipids. Ignoring stored vacuolar phosphorus, cellular phospholipids can account for up to a third of organic phosphorus in cells (in the order of RNA > phospholipids > phosphate-esters > DNA > phosphorylated proteins) and therefore represent a major proportion of the phosphorus budget<sup>[32,33]</sup>. Adaptive metabolic responses that release these stores can make a major contribution to plant adaptation to growth under low-phosphorus conditions and represents a target for improving crop phosphorus use efficiency. In phosphorus-deficient plants, the amounts of glycolipids increase at the expense of membrane phospholipids, e.g., phosphatidylcholine. The replacement of membrane phospholipids by glycolipids represents one of the most prominent changes in higher plants in response to phosphorus limitation.

Strategies for the remobilization of acquired phosphorus enable plants to maximize growth and biomass. Severe phosphorus-limitation triggers the replacement of up to half the membrane phospholipids with phosphorus-free galactolipids, i.e., mono or digalactosyl diacylglycerol and sulfoquinovosyl diacylglycerol (Fig. 3). Metabolic adaptation and membrane remodeling enables plants to adapt to extremely low-phosphorus environments<sup>[33,34]</sup>. Yet the fundamental understanding of the processes underpinning membrane lipid exchange in crops remains limited. Membrane remodeling is critical to plant performance during phosphorus stress and has been demonstrated by knockout studies in *Arabidopsis thaliana*<sup>[35]</sup>.

Beyond model species, changes in phospholipases are part of a complex transcriptional response that crops, e.g.,



**Fig. 3** Leaf lipid remodeling in response to growth at low soil phosphorus. PL, phospholipids; PLD, phospholipase D; PLC, phospholipase C; NPC5, non-specific phospholipase C5; PA, phosphatidic acid; PAH, phosphatidic acid phosphohydrolase; DAG, diacylglycerol; MGDG, monogalatosyldiglycerol; MGDGS, monogalactosyl diacylglycerol synthase; DGDG, digalactosyldiacylglycerol; DGDGS, digalactosyldiacylglycerol synthase; SQD2, sulfolipid synthase; SQDG, sulphoquinovosyl-diglyceride.

brassica species, use to manipulate membrane lipids and enhances phosphorus recycling<sup>[36]</sup>. Transcripts involved in the catabolism of phospholipids and the biosynthesis of galactolipids/sulfolipids accumulate to significantly greater abundance, while the production of phospholipids is reduced. The combined analysis of the transcriptome and lipidome in two rice genotypes with different degrees of tolerance to low phosphorus availability confirmed that the Dular (low-phosphorus-tolerant genotype) had a stronger expression of lipid remodeling genes in the shoot and to a lesser extent in the roots, when compared to the PB1 low-phosphorus sensitive genotype<sup>[37]</sup>. Evidence indicates that transcriptional responses to phosphorus availability are highly heritable and provide potential targets for breeding crops with improved phosphorus use efficiency<sup>[38–41]</sup>.

## 11 Intercropping

In addition to improving the use of organic and residual phosphorus in soils, another method for better utilization of soil phosphorus is intercropping, where two or more species are grown in close proximity, rather than in monocultures<sup>[42]</sup>. To test this, we grew ryegrass and white clover either as monocultures or as a mixed sward with a 3:1 ratio of grass to clover, but with the same total seed mass as the monocultures. Mixed swards had an 18%–35% increase in yield compared to that predicted from the monoculture yields, but there was no significant effect on the phosphorus concentration of the sward. Consequently, phosphorus uptake by the mixed sward was 22%–26% greater than in the monocultures. The cause of the increased phosphorus use efficiency in the mixed sward may be facilitation, whereby one plant increases the

availability of phosphorus and the other benefits, or a reduction in competition, because the two species are able to access different pools of phosphorus or access different physical locations within the soil<sup>[43]</sup>.

There are many other approaches, techniques and technologies that can improve phosphorus use efficiency that are not covered here, such as fertilizer placement, foliar sprays and modified root architecture, to name but a few, and no doubt novel approaches will continue to be developed. There is considerable uncertainty about the significance of the relative roles of plant traits and soil microbial communities, as well as soil invertebrates, and further investigations may yield novel insights.

## 12 Conclusions

Future phosphorus fertilizer availability is one of the most critical issues related to global food security and the sustainable intensification of agriculture that is required to achieve it. There are many opportunities for improving phosphorus use efficiency in agriculture in order to make the current sources of phosphorus fertilizer last longer, and also to prevent waste and losses to surface waters, and subsequent eutrophication. We suggest that some of the key areas that should be targeted as part of a wider effort to improve phosphorus use efficiency are as follows.

(1) Refining phosphorus fertilizer application recommendations by:

- a. Using the most appropriate soil test for individual soils to understand phosphorus availability.
- b. Improving understanding of the fate of added phosphorus and subsequent availability in specific soil types, e.g., apportionment and speciation of added phosphorus in soils and plants.
- c. Incorporating organic phosphorus into soil tests.
- d. Changing the philosophy from maintaining soil phosphorus status at a relatively high index to a lower index.
- e. Establishing soil by crop-specific critical phosphorus application rate recommendations.

(2) Managing soil pH to optimize availability of soil phosphorus.

(3) Developing novel and recycled phosphorus fertilizers to reduce the reliance on rock phosphate for phosphorus fertilizers.

(4) Developing plant traits for phosphorus use efficiency, especially:

- a. Remodeled membrane lipids that lower the phosphorus requirements of plants.
- b. Root morphology that enables plants to more efficiently scavenge soils for phosphorus.
- c. Root exudates that mobilize and hydrolyze phosphorus not immediately available to plants, and thus exploit the accumulated phosphorus in soils arising from historic phosphorus applications.

(5) Developing phosphorus-efficient cropping systems such as intercropped swards, and other novel cropping systems or combinations.

As well as the specific points listed above, some fundamental issues still need to be addressed. These include improved understanding of the relative roles of plants versus microbes in the cycling and the availability of soil phosphorus, to facilitate better management. Also, improvement and maintenance of soil structure will have significant impacts. Basic issues such as access to phosphorus fertilizers by farmers in terms of both affordability and availability are still fundamental issues, and likely to remain so in the future, but the development of novel fertilizers that are sourced locally could help remedy this. Of course, tackling these issues and developing more knowledge to enable this will require considerable investment in research, technology and sometimes infrastructure. Given the potentially imminent issue of phosphorus fertilizer availability in some parts of the world and the growing pressures on global food security, it is now important that a concerted effort to increase phosphorus use efficiency is prioritized.

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