Annals of Botany **129**: 247–258, 2022
https://doi.org/10.1093/aob/mcab145, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
Founded 1887

REVIEW

Mechanisms for improving phosphorus utilization efficiency in plants

Yang Han[1], Philip J. White[2] and Lingyun Cheng[1,*]

[1]College of Resources and Environmental Sciences; National Academy of Agriculture Green Development; Key Laboratory of Plant-Soil Interactions, Ministry of Education, China Agricultural University, Beijing 100193, PR China and [2]Department of Ecological Sciences, The James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK
** For correspondence. E-mail lycheng@cau.edu.cn*

Received: 11 November 2021 Returned for revision: 14 October 2021 Editorial decision: 24 November 2021 Accepted: 2 December 2021
Electronically published: 4 December 2021

• **Background** Limitation of plant productivity by phosphorus (P) supply is widespread and will probably increase in the future. Relatively large amounts of P fertilizer are applied to sustain crop growth and development and to achieve high yields. However, with increasing P application, plant P efficiency generally declines, which results in greater losses of P to the environment with detrimental consequences for ecosystems.
• **Scope** A strategy for reducing P input and environmental losses while maintaining or increasing plant performance is the development of crops that take up P effectively from the soil (P acquisition efficiency) or promote productivity per unit of P taken up (P utilization efficiency). In this review, we describe current research on P metabolism and transport and its relevance for improving P utilization efficiency.
• **Conclusions** Enhanced P utilization efficiency can be achieved by optimal partitioning of cellular P and distributing P effectively between tissues, allowing maximum growth and biomass of harvestable plant parts. Knowledge of the mechanisms involved could help design and breed crops with greater P utilization efficiency.

Key words: Phosphorus, phosphorus utilization efficiency, phosphorus pools, phosphorus recycling, phosphorus distribution.

INTRODUCTION

Phosphorus (P) is an essential macronutrient required for plant development and reproduction (White and Hammond, 2008; Hawkesford *et al*., 2012). However, an acute conflict in modern agriculture arises between increasing demand for agricultural output and inefficient application of non-renewable P as a fertilizer (Miao *et al*., 2011; Yan *et al*., 2021). The low concentration and poor mobility of plant-available phosphate (Pi) in soils greatly limits plant growth and crop production (Raghothama and Karthikeyan, 2005; Shen *et al*., 2011; Kochian, 2012; Sun *et al*., 2018). To alleviate such restrictions, P-containing fertilizers are applied in many agroecosystems, but only 20–30 % of the P applied is taken up by plants during the first year after application (Vance *et al*., 2003; Richardson and Simpson, 2011). This situation leads to P-runoff from soils, contributing to an enrichment of water bodies with P that causes eutrophication and toxic algal blooms in aquatic ecosystems (Zak *et al*., 2018). Moreover, P in mineral fertilizers is mainly obtained from phosphate rock, which is a non-renewable resource (Dawson and Hilton, 2011). Therefore, the development of P-efficient cultivars that produce high yields with reduced fertilizer inputs is seen as an important strategy for sparing global P resources and minimizing environmental problems.

Plants can improve P efficiency by enhancing P acquisition efficiency (PAE, the ability of plants to take up P from the soil) or P utilization efficiency (PUE, the capacity of plants to use the P acquired to generate biomass or yield) (Hammond *et al*., 2009; Rose *et al*., 2011; White *et al*., 2013; Wu *et al*., 2013; Dissanayaka *et al*., 2018). In the past few decades, the focus has been on improving PAE. This is related to: (1) root system architecture, such as higher root density and more lateral root branches enabling roots to take up more P from the topsoil (Hammond *et al*., 2009; George *et al*., 2011; Lynch, 2011, 2019; White *et al*., 2013; Jia *et al*., 2018; Sun *et al*., 2018; Wang *et al*., 2019); (2) enhanced root exudation of protons, organic anions and enzymes that facilitate the solubilization of soil P (Pang *et al*., 2018; Robles-Aguilar *et al*., 2019; Wen *et al*., 2019); and (3) interactions with microorganisms, such as arbuscular mycorrhizal fungi that enlarge the soil volume exploited for P acquisition (Yang *et al*., 2012; Zhang *et al*., 2018) or phosphate-solubilizing bacteria that increase soil P availability (Zhang *et al*., 2016). Increasing the acquisition of P benefits crop production and reduces soil P runoff, but it will also increase the total amount of P removed from the field in plant biomass, resulting in a depletion of soil P reserves. In addition, increasing P uptake will also increase the accumulation of P in the form of phytate in seeds, which might cause off-site environmental problems. For example,

phytate cannot be digested by monogastric animals and is excreted into rivers and lakes, causing eutrophication of water bodies (Yamaji *et al*., 2017; Lynch, 2019; Che *et al*., 2020). In addition to improving PAE, complementary improvements in crop physiology to maximize PUE, which allow the reduction of P-fertilizer inputs and P offtakes from the field, are needed to secure food production while protecting P and water resources (Hammond *et al*., 2009).

In the past few years, considerable advances have been made towards understanding how plants adapt to low-P stress and the mechanisms that increase P utilization. In this review, we summarize and discuss relevant information on the remobilization of liberated Pi from source to sink, including vegetative–vegetative and vegetative–reproductive P fluxes, the contribution of cell-specific P allocation to plant PUE, and the processes releasing Pi from inorganic and organic P pools in the plant. This information can contribute to new approaches for developing crops with greater PUE.

(RE)DISTRIBUTION OF PI BETWEEN TISSUES

When plants lack sufficient P, they mobilize Pi from older leaves to maintain resource acquisition through photosynthesis of younger leaves and nutrient uptake by roots (Hammond *et al*., 2003). Plants catabolize a variety of organic P compounds in both non-senescent and senescent tissues (see 'Remobilizing phosphorus from cellular pools' below). The Pi released must be transported to younger tissues to maintain photosynthesis and plant growth during the vegetative stage (Veneklaas *et al*., 2012). When plants enter the reproductive stage, Pi must be transported to seeds. The coordinated activity of Pi transporters is required to control Pi fluxes from older leaves to younger leaves during vegetative growth and from leaves to grains during reproductive growth. Considerable progress has been made recently in identifying the molecular mechanisms of Pi transport within plants. Here, we summarize our knowledge of the Pi transporters involved in source-to-sink Pi transport (as shown in Table 1) and the contribution of different P pools in cells to PUE.

Enhancing Pi transport from source to sink during vegetative growth

A group of well-studied Pi transporters belonging to the *Pht1* family are expressed in both roots and shoots (Karthikeyan *et al*., 2002; Nagarajan *et al*., 2011). The majority of these are induced by P deficiency and catalyse Pi transport from source to sink organs (Table 1). For example, low-affinity Pi transporters, such as *AtPht1;5* from Arabidopsis and *HvPht1;6* from barley, are induced in leaves by P deficiency and play a critical role in transporting Pi between source and sink organs (Rae *et al*., 2003; Nagarajan *et al*., 2011). Similarly, a marked induction of *GmPT1* transcript was observed in young leaves, mature leaves and roots during long-term P deficiency, which promoted Pi remobilization in soybean plants (Song *et al*., 2014). Overexpressing *GmPT1* in tobacco increased total plant dry weight, PUE and grain yield (Song *et al*., 2014). In rice (*Oryza sativa*), *OsPht1;8*, a high-affinity Pi transporter, is responsible for Pi transport from older to younger leaves and an *Ospht1;8* RNA interference (RNAi) line reduced the accumulation of Pi in old blades and panicle axis (Li *et al*., 2015). *OsPht1;4* is also induced by P deficiency and the downregulation of *OsPht1;4* reduced the concentration of Pi in flag leaves and xylem sap (Ye *et al*., 2015; Zhang *et al*., 2015), suggesting that *OsPht1;4* plays a role in re-mobilizing Pi in rice. Similarly, *OsPht1;3* is induced by P deficiency and acts in the redistribution of Pi in rice grown under P-deficient conditions (Chang *et al*., 2019). Mutation of *Ospht1;3* led to a significant decrease in Pi accumulation in the youngest leaf and an increase in Pi accumulation in basal nodes (Chang *et al*., 2019). Wang *et al*. (2020) reported that *ZmPT7*, a close homologue of *OsPht1;8*, was mainly expressed in bundle sheath cells and phosphorylated in old leaves by P deficiency.

Table 1. *Transporters involved in P transport from source to sink during the vegetative or reproductive stage.*

	Gene	Species	Expression tissue(s)	Function(s)	Reference
Vegetative stage	*Pht1;1*	*Glycine max* L. Merr.	Roots, leaves, stems, flowers	P remobilization from source to sink leaves, increase PUE and soybean yield	Song *et al*. (2014)
	Pht1;3	*Oryza sativa* L.	Phloem regions of both RVB and EVB	P remobilization from source to sink leaves	Chang *et al*. (2019)
	Pht1;4	*Oryza sativa* L.	Flag leaves, ligules, nodes, internodes	P remobilization from flag leaf to panicles	Ye *et al*. (2015), Zhang *et al*. (2015)
	Pht1;5	*Arabidopsis thaliana*	Roots, leaves	P remobilization from source to sink leaves	Nagarajan *et al*. (2011)
	Pht1;6	*Hordeum vulgare* L.	Flag leaves, old leaves	Remobilization of stored P from leaves	Rae *et al*. (2003)
	Pht1;7	*Zea mays* L.	Roots, leaves	P remobilization from source to sink leaves	Wang *et al*. (2020)
	Pht1;8	*Oryza sativa* L., *Triticum aestivum* L.	Roots, leaves, stems, seeds	P remobilization from source to sink leaves and seeds	Li *et al*. (2015)
Reproductive stage	*SPDT*	*Oryza sativa* L.	Xylem region of vascular bundles of nodes	Increasing the distribution of P from leaves to grain	Yamaji *et al*. (2017)
	Pho1;1	*Oryza sativa* L.	Phloem region of DVBs of node I	Loading P into the phloem of DVBs and allocate to grains	Che *et al*. (2020)
	Pho1;2	*Oryza sativa* L. *Zea mays* L.	Xylem region of EVBs of node I	Unloading P from the xylem of EVBs	Che *et al*. (2020); Ma *et al*. (2021)

Abbreviations: Pht, phosphate transporter; SPDT, SULTR-like phosphorus distribution transporter; Pho, phosphate; EVBs, enlarged vascular bundles; DVBs, diffuse vascular bundles; RVBs, regular vascular bundles; PUE, phosphorus utilization efficiency.

The phosphorylation of *ZmPT7* enhanced Pi transport capacity from old leaves to young leaves.

Preferential allocation of Pi to photosynthetic leaf cells

During vegetative growth, different leaf cell types have different physiological functions, and the partitioning of nutrients to different leaf cells is element-specific and affected by plant variety, growth stage and external environment (Conn and Gilliham, 2010). The allocation of P and calcium to different leaf cells reduces the formation of insoluble P compounds. Mesophyll cells are located between the upper and lower leaf epidermis and contain many chloroplasts that are responsible for most photosynthesis in plants (Braun and Slewinski, 2009). Phosphate is incorporated into ATP by thylakoid ATP synthases and transferred to the phosphorylated intermediates of the Calvin cycle, and released again during the synthesis of final products, such as sucrose, starch and amino acids, consequently returning to the chloroplast in strict exchange with triose-P (Stitt *et al*., 2010). In eudicots, P is often, but not always, preferentially allocated to epidermal cells, while in monocots, it is preferentially allocated to mesophyll cells (Fricke *et al*., 1994; Karley *et al*., 2000; Conn and Gilliham, 2010; Carvalho *et al*., 2016; Pongrac and White, 2017; Hayes *et al*., 2018). The preferential allocation of P to photosynthetic tissues might be a general adaptation improving PUE in extremely P-impoverished habitats (Hayes *et al*., 2018; Pereira *et al*., 2018). Large amounts of Pi are required within the mesophyll layers for ribosomal RNA (rRNA) to sustain the synthesis of photosynthetic proteins, for phospholipids (PLs), for phosphorylated intermediates of carbon metabolism and for the export of triose phosphate from chloroplasts (Flügge and Heldt, 1991; Veneklaas *et al*., 2012). Thus, the preferential allocation of P to mesophyll cells allows greater photosynthetic PUE in photosynthetic carbon metabolism, especially when P is scarce. In addition, species adapted to extremely P-impoverished habitats, such as Proteaceae species, exhibit slow development of the photosynthetic apparatus ('delayed greening'), with young leaves having very low levels of chlorophyll and Calvin–Benson cycle enzymes, which may contribute to PUE (Sulpice *et al*., 2014). In young, expanding leaves of Proteaceae there is a particularly low investment in plastidic rRNA, which is accompanied by a delay in chloroplast biogenesis. Delayed greening separates leaf growth and chloroplast biogenesis, allowing the sequential use of the P invested in ribosomes. Thus, P can be allocated first to leaf growth and expansion, and then to the development of the photosynthetic machinery, thereby increasing PUE (Kuppusamy *et al*., 2020).

The mechanisms responsible for P allocation to different leaf cell types and its consequences for developing P-efficient crop varieties are unknown. Nevertheless technologies, including X-ray fluorescence microscopy, laser ablation inductively coupled plasma mass spectrometry, scanning electron microscopy coupled with energy-dispersive X-ray spectroscopy, and autoradiography with radioactive isotopes (Zhao *et al*., 2014; Carvalho *et al*., 2016; Kopittke *et al*., 2018), and their integration with molecular biology provides opportunities to address this knowledge gap.

Reducing Pi transport from source to sink during the reproductive stage without affecting yield

During the reproductive stage, ~60–85 % of P in a cereal is allocated to grain, resulting in a large P offtake from farmland in grain (Raboy, 2001; Che *et al*., 2020). El Mazlouzi *et al*. (2020) quantified the source of P in wheat grains by introducing a ^{32}P tracer after anthesis. Their results showed that 65 % of grain P was contributed by the remobilization of P from vegetative tissue when P supply was high, and this increased to 81 % when P supply was limited.

A certain amount of seed P, stored mainly as phytate, is necessary to supply the P required for germination and seedling establishment (White and Veneklaas, 2012), but seed P can exceed these requirements when plants receive a high P supply, and is arguably less important in modern agricultural systems that apply P fertilizer close to the seed prior to germination (Burns *et al*., 2010; Rose *et al*., 2012; Wang *et al*., 2021). Hence, there appears to be potential to identify, and breed for, the minimal seed P content that has no effect on seed germination, seedling establishment or yield in a given agroenvironment to improve PUE.

The delivery of P to the seed is determined by the P concentration in the phloem and the rate of phloem transport. The P concentration in the phloem is determined by the loading of Pi into the phloem in the source leaf, whilst the rate and direction of phloem transport is determined by the unloading of photosynthate in the seed (White, 2012). Recent studies have revealed several Pi transporters that play important roles in Pi transport to grain (Table 1). Yamaji *et al*. (2017) found a gene with high expression induced by low P in the node (the junction between flag leaf and panicle) of rice and named it *SPDT* (SULTR-like phosphorus distribution transporter). Knocking out *SPDT* had no significant effect on yield, but changed the distribution of P among different organs greatly. In the wild-type, 64.5 % of total P in above-ground parts was allocated to brown rice grain, while in mutants this was only 42.5–44.0 %, and the P concentration in grain of the mutants was about 20 % less than in wild-type plants, suggesting that *SPDT* regulated the distribution of P between leaves and grain. Recent studies have revealed that OsPHO1;2, a PHO1-type Pi transporter, plays an important role in Pi reallocation during grain filling (Ma *et al*., 2021). Mutation of *Ospho1;2* leads to excessive accumulation of P in seeds and inhibits the activity of ADP-glucose pyrophosphorylase (AGPase), which is essential for starch synthesis. In contrast, *OsPHO1;2* overexpression lines not only showed a reduction in P accumulation in developing seeds but also greater AGPase activity and grain yield (Ma *et al*., 2021). The development of new technologies, particularly the combination of transcriptomics, metabolomics, proteomics, ionomics, genome-wide association studies and molecular biology, will provide more information on the regulatory networks of P distribution to grain that might be co-opted to improve PUE and reduce P loss in the food chain.

Phytate, the main form of P in grains (White and Broadley, 2009), cannot be digested by humans or monogastric livestock and might be discharged into the environment in the form of sewage or faeces without proper wastewater management measures (Abbasi *et al*., 2019). In addition, phytate is chelated with zinc and iron in grains, reducing the availability of

these essential elements and the nutritional quality of grains (White and Broadley, 2009; Murgia *et al*., 2012; Raboy, 2020). Reducing the accumulation of phytate in grains and allocating P to tissues where it contributes to resource acquisition and plant growth are potential strategies for reducing P removal from the field and improving PUE (Yamaji *et al*., 2017). However, mutants with reduced grain phytate concentrations are often compromised in seedling vigour and subsequent crop yield (Raboy, 2009; Robinson *et al*., 2012*a*; Pariasca-Tanaka *et al*., 2015), although recent studies in rice and chickpea found that a low seed P concentration does not affect seedling vigour when external soil P fertility is sufficient or when adequate starter P-fertilizer is applied (Rose *et al*., 2012; Wang *et al*., 2021). Thus, reducing seed P concentrations in crops appears to be a potential strategy to improve PUE. Further research might focus on combining genetic and agronomic strategies to enable a reduction in phytate and P concentrations in grain whilst maintaining crop yield.

REMOBILIZING PHOSPHORUS FROM CELLULAR POOLS

Phosphorus in plant cells exists either as Pi or as organic P (White and Hammond, 2008; Veneklaas *et al*., 2012). When plants cannot acquire sufficient P to meet their immediate requirements for growth, vacuolar Pi is released to maintain cytoplasmic Pi concentration and normal cellular functions (Lee *et al*., 1990; White and Hammond, 2008; Pratt *et al*., 2009). In addition, the replacement of plant membrane PLs by non-PLs, the substitution of phosphorylated metabolites with metabolites that require less P, and the reduction of ribosome number to optimize the protein synthesis system can provide strategies to improve P utilization during plant P deficiency (White and Hammond, 2008; Plaxton and Tran, 2011; Lambers *et al*., 2012; Veneklaas *et al*., 2012; Sulpice *et al*., 2014; Siebers *et al*., 2015; Prodhan *et al*., 2019). Here, we summarize the implications of these processes for developing plants with greater PUE.

Phosphate recycling from vacuoles

Phosphate is fundamental to virtually all cellular metabolism in plants, and Pi concentrations regulate phosphorylated carbohydrate metabolism, photosynthesis and respiration (Hammond and White, 2008; White and Hammond, 2008; Pratt *et al*., 2009). The vacuole is a major Pi pool and, in P-replete plants, can contribute as much as 85 % of the cellular Pi in vegetative tissues (Bieleski, 1973; White and Hammond, 2008; Veneklaas *et al*., 2012). Cellular Pi homeostasis depends on shuttling Pi between the cytosol and vacuoles (Veneklaas *et al*., 2012). When P is sufficient, excess Pi is taken up and stored in vacuoles for remobilization upon P deficiency. The ability to release Pi from vacuoles is important for adapting to intermittent low-P stress (Liu *et al*., 2015). Significant progress has been made in identifying the tonoplast Pi transporters responsible for shuttling Pi between vacuoles and the cytosol in model plants, such as Arabidopsis and rice (Liu *et al*., 2015, 2016; Wang *et al*., 2015; Xu *et al*., 2019).

In Arabidopsis, vacuolar Pi transporters [VPTs; also named the Pi transporter type 5 (PHT5) family] transport Pi from the cytosol to the vacuolar lumen (Liu *et al*., 2015, 2016; Srivastava *et al*., 2018). A *VPT1* (*Pht5;1*) mutation in Arabidopsis leads to low vacuolar Pi concentrations, as well as a low vacuole/cytoplasmic Pi quotient compared to wild-type plants (Liu *et al*., 2015, 2016). The *vpt1*/*vpt3* double mutants exhibit an excessive Pi allocation to floral organs rather than storing Pi in the vacuoles of leaf cells and have impaired development of siliques under P-sufficient conditions (Luan *et al*., 2019), further suggesting that VPTs contribute to regulating the dynamic balance of Pi during the reproductive stage through their function in vacuolar Pi sequestration (Luan *et al*., 2019). The rice homologues of *PHT5*, *OsSPX-MFS1*, *OsSPX-MFS2* and *OsSPX-MFS3*, are located on the tonoplast and *OsSPX-MFS3*-overexpressing lines had reduced vacuolar Pi concentration, suggesting that OsSPX-MFS3 mediates Pi efflux from vacuoles (Wang *et al*., 2015). In contrast, *OsSPX-MFS1* functions as a vacuolar Pi influx transporter (Wang *et al*., 2015; Liu *et al*., 2016). Xu *et al*. (2019) identified two vacuolar phosphate efflux transporters in rice: Vacuolar Phosphate Efflux Transporter 1 (OsVPE1) and OsVPE2. Overexpression of either *OsVPE1* or *OsVPE2* in transgenic rice reduced the vacuolar Pi concentration, demonstrating that OsVPE1 and OsVPE2 function as major vacuolar Pi efflux transporters (Xu *et al*., 2019). When plants are starved of P, the depletion of vacuolar Pi stored in *vpe* mutants was slower than in wild-type plants, resulting in delayed supply of Pi to the cytoplasm and early onset of P-starvation-induced gene expression (Luan and Lan, 2019; Xu *et al*., 2019). These findings indicate that OsVPE transporters mediate vacuolar Pi efflux and play an important role in recycling vacuolar Pi into the cytoplasm to satisfy cellular Pi requirements for plant growth in P-deficient plants.

Scavenging Pi from organic P fractions to improve PUE

When plants are deprived of P for extended periods and vacuolar Pi is depleted, there is a sharp decline in cytoplasmic Pi (Vance *et al*., 2003; Plaxton and Tran, 2011). Reapportionment of organic P fractions is necessary to support plant growth and development when vacuolar Pi is exhausted (Lambers *et al*., 2015*b*). Organic P in plants can be divided into four major fractions: (1) lipid-P; (2) low-molecular-mass Pi esters (ester-P); (3) nucleic acid-P (RNA-P and DNA-P); and (4) residual-P (phosphorylated proteins and unidentified residues, which mainly serve a regulatory function and contain small amounts of P; this will not be considered further) (Veneklaas *et al*., 2012; Mo *et al*., 2019). The size of organic P pools usually decreases in the order RNA-P > lipid-P > P-ester > DNA-P (Veneklaas *et al*., 2012). While the distribution of P among the main organic P pools differs slightly among species, it is affected more by the P status of the plant (Chapin and Bieleski, 1982; Veneklaas *et al*., 2012; Hidaka and Kitayama, 2013; Mo *et al*., 2019; Yan *et al*., 2019). Studies on barley showed that Pi accounted for 79 % of total P at a high P supply (100 μmol L^{-1}) and was mainly stored in vacuoles, whereas nucleic acid-P, lipid-P and ester-P accounted for 13, 4 and 4 % of total P, respectively (Chapin and Bieleski, 1982). In contrast, nucleic acid-P, lipid-P and ester-P accounted for 42, 14 and 23 % of total P, respectively, at a low P supply (1 μmol L^{-1}) (Chapin and Bieleski, 1982).

Lipids are the main components of plant membranes, and mainly comprise PLs, glycolipids and sulpholipids. It is argued that PLs could comprise up to 30 % of the total cellular organic P pool that might be hydrolysed when vacuolar Pi concentrations are insufficient to meet plant demand (Lambers *et al*., 2012; Veneklaas *et al*., 2012). The dominant lipids in most plant membranes are PLs, but the thylakoid membranes of the chloroplast are uniquely enriched in galactolipids (monogalactosyldiacylglycerol, MGDG; digalactosyldiacylglycerol, DGDG) and sulpholipid (sulphoq uinovosyldiacylglycerol, SQDG) (Harwood, 1989; Narayanan *et al*. 2018). The hydrolysis of PLs and their replacement by galactolipids and sulpholipids is an important strategy for plants to improve PUE without damaging membrane integrity or function (Tjellström *et al*., 2008; Stigter and Plaxton, 2015; Lambers *et al*., 2015*b*; Dissanayaka *et al*., 2018). PLs in other cell membranes can also be replaced, to a limited extent, by galactolipids and sulpholipids, although the effects of this replacement on membrane function in plants is largely unknown (Veneklaas *et al*., 2012). However, in Proteaceae species adapted to the extremely P-impoverished habitats of south-western Australia, PLs are replaced extensively by galactolipids and sulpholipids while the leaves still maintain a high photosynthetic rate (Denton *et al*., 2007; Lambers *et al*., 2011, 2015*a*). The replacement of PLs by galactolipids and sulpholipids appears to be a ubiquitous response of plants to low P supply (Tjellström *et al*., 2008; Plaxton and Tran, 2011). For example, the replacement of PLs by DGDG has been reported to occur in Arabidopsis (Härtel *et al*., 2000), oat (Andersson *et al*., 2003), soy bean (Gaude *et al*., 2004) and bean (Russo *et al*., 2007).

Young leaves must maintain a high PL content to protect the integrity of membranes during cell division and elongation, while PLs can be replaced by galactolipids and sulpholipids in older leaves (Lambers *et al*., 2015*a*). In the process of membrane remodelling, phospholipase C catalyses PL hydrolysis, resulting in diacylglycerol (DAG) and a polar group phosphocholine, which is further hydrolysed by acid phosphatase (APase) to liberate Pi (Dissanayaka *et al*., 2018). Phospholipase D catalyses PL hydrolysis, resulting in choline and phosphatidic acid, which can be further hydrolysed by APase to DAG to liberate Pi (Wang, 2000; Dissanayaka *et al*., 2018). In addition, PLs can be deacylated by phospholipase A and lysophospholipase into glycerophosphocholine and glycerophosphoinositol, which can then be hydrolysed by P deficiency-induced glycerophosphodiester phosphodiesterases (GPX-PDEs or GDPDs) to glycerol-3-phosphate (G3P) and choline or inositol; G3P is then hydrolysed by APase to release Pi and glycerol (Cheng *et al*., 2011*a*, b; Dissanayaka *et al*., 2018). In Arabidopsis, non-specific phospholipase C5 (NPC5) is involved in the degradation of membrane PLs under P deficiency and promotes DGDG synthesis and Pi release (Gaude *et al*., 2008). Another recently identified enzyme involved in PL hydrolysis and remodelling in Arabidopsis, NCP4, is induced during P starvation and hydrolyses glycosylinositolp hosphorylceramide to release Pi (Yang *et al*., 2021). In rice, *OsGDPD2*-overexpressing lines have greater tillering, shoot biomass and Pi content under P deficiency than wild-type plants. Monogalactosyldiacylglycerol and DGDG contents of *OsGDPD2*-overexpressing lines were 2.2- and 2-fold higher than in wild-type plants, respectively (Mehra *et al*., 2019). Wang *et al*. (2021) identified two *GPX-PDE* genes in maize induced by P deficiency that degrade glycerophosphodiester to allow Pi recycling from senescent leaves to young leaves.

Low-molecular-mass Pi esters (ester-P) are a major P fraction involved in cellular metabolic processes, including cytosolic glycolysis, mitochondrial respiration and photosynthesis (Hawkesford *et al*., 2012). They include adenosine diphosphate, adenosine triphosphate and sugar phosphates (Lambers *et al*., 2015*b*; Ye *et al*., 2018), which generally comprise 15–21 % of total P in most plants (Veneklaas *et al*., 2012). Ester-P are the target of purple acid phosphatases (PAPases) whose activities improve PUE by liberating Pi from ester-P over a wide pH range during P starvation (Plaxton and Tran, 2011). Many PAPases have been identified, with the Arabidopsis, rice, soybean and maize genomes encoding 29, 26, 35 and 33 putative genes encoding PAPases, respectively (Li *et al*., 2002; Zhang *et al*., 2011; Li *et al*., 2012; González-Muñoz *et al*., 2015). AtPAP26 is an important PAPase isozyme that is upregulated by P deficiency and mediates the scavenging of Pi from ester-P during P starvation and leaf senescence to improve PUE (Veljanovski *et al*., 2006; Hurley *et al*., 2010; Tran *et al*., 2010; Robinson *et al*., 2012*a*, *b*). A mutation in *AtPAP26* reduced P remobilization from senescing leaves by 55 % compared to the wild-type allele (Robinson *et al*., 2012*a*). Similarly, *OsPAP26*, the homologous gene to *AtPAP26*, is also upregulated during P starvation and scavenges Pi from ester-P in rice (Gao *et al*., 2017). In senescing leaves of *Hakea prostrata*, a native plant adapted to extremely P-impoverished soil in south-western Australia, greater intracellular PAPase activity was correlated with efficient Pi remobilization, providing further evidence for the role of PAP26 in scavenging Pi during leaf senescence (Shane *et al*., 2014). In Arabidopsis, *AtSgpp* encodes a typical phosphomonoesterase with a wide range of sugar phosphate substrates that is expressed in most tissues and plays a role in liberating Pi from sugar phosphates (Caparrós-Martín *et al*., 2013). Similarly, *AtPPsPase1* (*pyrophosphate-specific phosphatase1*) encodes an inorganic pyrophosphatase that is induced by P starvation and scavenges Pi from pyrophosphate when cytosolic Pi concentrations become critically low (May *et al*., 2011). All these phosphatases play important roles in scavenging Pi from a wide range of ester-P to improve PUE when P supply is low.

Nucleic acid-P accounts for the largest proportion of organic P in plants under severe P deficiency, and most of it is in rRNA (Veneklaas *et al*., 2012). Nucleic acids play a fundamental role in DNA replication, protein synthesis and RNA signalling, impacting plant metabolism, including photosynthesis, growth and development (Raven, 2012, 2015; Ellsworth *et al*., 2015). Developing leaves require a large amount of P-rich rRNA to maintain a protein synthesis rate compatible with fast growth, whereas senescent leaves reduce protein synthesis and accelerate the degradation of RNA and finally DNA (Matzek and Vitousek, 2009; Lovelock *et al*., 2014). Phosphorus limitation reduces rRNA content, thereby limiting the growth of plants (Hewitt *et al*., 2005). Nevertheless, economizing on the use of RNA-P and maximizing Pi release from the rRNA pool might improve PUE. Raven (2013) discussed three possibilities of economizing P use in RNA: (1) reducing the ribosome

abundance of organs to adapt to the maximum protein synthesis rate, (2) maintaining a constant protein synthesis rate throughout the life cycle and (3) minimizing the degree of protein turnover. Developing leaves of Proteaceae growing in P-impoverished soils had low rRNA content and delayed greening, which confers greater PUE by reducing the investment of P in rRNA and separating leaf growth and chloroplast biogenesis (Sulpice *et al*., 2014). However, Proteaceae grow slowly in their native environments and achieving rRNA economies in crop plants must be compatible with their fast growth rates (Lambers *et al*., 2011). How reduced ribosome number would affect the growth and yield of crop plants with fast growth rates in high-input environments needs to be investigated.

The degradation of rRNA is mainly initiated by RNases, such as those belonging to the RNase T2 family, which is composed of two subfamilies: S-RNases and S-like RNases (Bariola *et al*., 1999; MacIntosh *et al*., 2010). RNase T2 enzymes can catabolize RNA into nucleotide monophosphates (NMPs) via a 2′,3′-cyclic nucleotide monophosphate intermediate (cNMP), which can be hydrolysed by a cyclic nucleotide phosphodiesterase to produce an NMP and release Pi (Abel *et al*., 2000; Stigter and Plaxton, 2015). The first class of S-like RNases, such as RNaseLE and RNaseLX in tomato and RNS1 in Arabidopsis, are induced by P starvation and scavenge Pi from RNA to alleviate P limitation (Köck *et al*., 1995; Bariola *et al*., 1999; Hillwig *et al*., 2011). The second class of S-like RNases, including AtRNS2 and AhSL28, are also induced during P starvation (Liang *et al*., 2002; Hillwig *et al*., 2011), but not all class II RNases can release Pi, an example being RNaseLER of tomato (Köthke and Köck, 2011).

Organelle DNA also constitutes a substantial organic P pool, which might be re-utilized when it is degraded. During leaf senescence, AtBFN1 has been shown to be involved in DNA catabolism (Farage-Barhom *et al*., 2011). Recent studies have revealed that exonuclease DPD1 can degrade DNA and release Pi from mitochondria and chloroplasts (Takami *et al*., 2018). The lack of DPD1 attenuated the remobilization of Pi from senescent leaves to young leaves (Takami *et al*., 2018). As a

Table 2. *Manipulations of phosphorus (P) transport and metabolic processes that affect plant productivity.*

Strategies	Approach and gene name	Protein identifier	Target plant	Physiological trait(s)	Phenotype(s)	Reference(s)
(Re)distribution of Pi between tissues	OE: *PHT1;5*	At2g32830	*Arabidopsis thaliana*	Mobilization of stored Pi out of old leaves	↑ Shoot biomass	Nagarajan *et al.* (2011)
	OE: *PT1*	GLYMA_10G186500	*Glycine max* L.Merr.	Enhanced Pi mobilization from old leaves	↑ Grain yield, ↑ PUE	Song *et al.* (2014)
	RNAi: *pht1;4*	AF536964	*Oryza sativa* L.	Prevention of Pi mobilization from old leaves	↓ Grain yield	Zhang *et al.* (2015)
	OE: *PHT1;7*	FJ814695	*Zea mays* L.	Enhanced Pi redistribution from old to young leaves	↑ Shoot biomass	Wang *et al.* (2020)
	RNAi: *pht1;8*	AF536968	*Oryza sativa* L.	Prevention of Pi mobilization from old leaves	↓ Plant height, ↓ 1000-grain weight, ↓ PUE	Li *et al.* (2015)
	OE: *OsPHO1;2*	LOC_Os02g56510	*Oryza sativa* L.	Reduction of Pi accumulation in grains	↑ Grain yield, ↑ PUE	Ma *et al.* (2021)
	Tos-17: *spdt*	LOC_Os06g0143700	*Oryza sativa* L.	Reduction of Pi accumulation in grains	→ Grain yield, ↑ PUE	Yamaji *et al.* (2017)
Remobilizing P from cellular pools	OE: *PHT5;1*	At1g63010	*Arabidopsis thaliana*	Pi sequestration in vacuoles	↓ Shoot fresh weight	Liu *et al.* (2016)
	DM: *vpe1/vpe2*	LOC_Os04g46880/ LOC_Os08g06010	*Oryza sativa* L.	Pi sequestration in vacuoles	↓ Shoot biomass, ↓ root biomass	Xu *et al.* (2019)
	T-DNA DM: *vpt1/vpt3*	At1g63010 At4g22990	*Arabidopsis thaliana*	Defective in Pi homeostasis	↓ Silique length, ↓ seed number	Luan *et al.* (2019)
	OE: *GDPD2*	LOC_Os02g31030	*Oryza sativa* L.	Remobilization of Pi from membrane phospholipids	↑ Tiller number, ↑ shoot biomass, ↑ PUE	Mehra *et al.* (2019)
	T-DNA: *npc5*	At3g03540	*Arabidopsis thaliana*	Reduced DGDG accumulation	↓ Fresh weight	Gaude *et al.* (2008)
	OE: *PAP10c*	LOC_Os12g44020	*Oryza sativa* L.	Increased acid phosphatase (APase) activity in leaves	↑ Tiller number, ↓ plant height	Lu *et al.* (2016)
	OE: *PAP26*	NA	*Oryza sativa* L.	Increased acid phosphatase (APase) activity and redistribution of Pi from older to younger leaves	↑ Biomass	Gao *et al.* (2017)
	T-DNA: *pap26*	At5g34850	*Arabidopsis thaliana*	Increased acid phosphatase (APase) activity	↓ Fresh weight	Hurley *et al.* (2010)
	T-DNA DM: *pap12/pap26*	At2g27190 At5g34850	*Arabidopsis thaliana*	Recycling Pi from endogenous phosphomonoesters	↓ Biomass, ↓ PUE	Robinson *et al.* (2012b)
	T-DNA: *dpd1*	At5g26940	*Arabidopsis thaliana*	Organellar DNA degradation and efficient use of Pi	↓ Seed number	Takami *et al.* (2018)

Abbreviations: PHT, phosphate transporter; SPDT, SULTR-like phosphorus distribution transporter; PHO, phosphate; VPE, vacuolar phosphate efflux transporter; VPT, vacuolar phosphate transporter; PAP, purple acid phosphatase; NPC, non-specific phospholipase; GDPD, glycerophosphodiester phosphodiesterase; DPD, DNA degradation; Pi, phosphate; PUE, phosphorus utilization efficiency; DM, double mutant.

potential source of cellular P, Pi-scavenging and re-use of P from organelle DNA needs to be studied further.

DEVELOPING CROPS WITH GREATER PUE

In modern crop production, the application of large amounts of P fertilizer leads to the accumulation of excessive P in the soil that causes environmental problems through the eutrophication of water bodies (Withers and Haygarth, 2007; White and Brown, 2010; Schoumans *et al*., 2014). By contrast, in less developed regions, resource-poor farmers may not have the financial means to purchase P fertilizers in sufficient quantities to balance P offtake from fields at harvest (MacDonald *et al*., 2011; Vandamme *et al*., 2016). Utilizing P more efficiently is crucial for sustainable crop production, to prevent environmental problems and to reduce the consumption of a non-renewable resource. The development of cultivars with greater PUE that produce high yields with reduced fertilizer inputs and acceptable yields in low-input systems is seen as an important component of future crop production systems (Veneklaas *et al*., 2012).

PUE is a complex agronomic trait, involving multiple interconnected steps of P metabolism and transport, that is synergistic with beneficial root and rhizosphere traits that improve PAE (which are not reviewed here). Many transgenic approaches have shown that manipulating the expression of genes involved in P metabolism or transport can enhance plant growth, seed yield or PUE (Table 2). Several studies have shown that the manipulation of Pi transporters mediating Pi mobilization in tissues is a feasible strategy for improving crop PUE. For example, overexpression of rice *GmPT1* improved grain yield and PUE through enhancing Pi mobilization from older to younger leaves (Song *et al*., 2014). By contrast, overexpression of *PHO1;2* in rice can lead to a reduction of Pi accumulation in grains and to increased grain yield and PUE (Ma *et al*., 2021). Transporters in the tonoplast can also contribute to PUE. For example, introducing *OsVPE1/VPE2* driven by a 35S promoter in rice increased vacuolar Pi sequestration and led to a reduced shoot biomass (Xu *et al*., 2019), suggesting that reducing tonoplast Pi transport activity might improve PUE. Manipulation of enzymes that mediate Pi mobilization from organic P pools also enhance yield and PUE. For example, overexpressing *GDPD2* enhanced Pi remobilization from membrane PLs and increased tiller number in rice (Mehra *et al*., 2019). Overexpression of *APases* also enhanced tiller number or biomass accumulation in rice (Lu *et al*., 2016; Gao *et al*., 2017).

To avoid deploying genetically modified organisms in the field, marker-aided molecular breeding strategies can be adopted to improve PUE. Breeding efforts in the past have focused disproportionally on improving PAE of crops (Wissuwa *et al*., 2009; Wang *et al*., 2019). Nevertheless, there have been some efforts to breed for increased PUE (Rose and Wissuwa, 2012). Most of the genetic loci impacting PUE have been identified in studies in which PUE was negatively associated with biomass as a consequence of poor P uptake of the parent with greater PUE (Wissuwa *et al*., 2015). Such quantitative trait loci (QTLs) are of little practical value. However, Wissuwa *et al*. (2015) identified a locus associated with both greater PUE and biomass production that has promise for use in breeding crops for improved PUE.

Employing a holistic view will enable molecular breeders to redesign crops by pyramiding genes or QTLs for multiple traits enhancing PUE. An ideal PUE variety would have optimal partitioning of cellular P and the ability to distribute P effectively between organs and within tissues, allowing maximum growth and biomass of harvestable parts. All these traits have so far been studied in isolation and with limited success in terms of producing the desired phenotype (Delhaize *et al*., 2001; Richardson *et al*., 2001, Wissuwa *et al*., 2015). The more difficult task of combining them into a single phenotype awaits realization. Furthermore, several of the individual successes presented in Table 2 were performed in pot or hydroponic systems. The next challenge is to establish whether growth behaviour observed in the laboratory or glasshouse can be reproduced in field trials and eventually be integrated into breeding programmes.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Increasing PAE or PUE will enable greater yields of crops grown in P-deficient soils and will also allow a reduction in the P-fertilizer input required to achieve optimal production on well-fertilized soils. The effect of increasing PUE on reducing the soil-available P concentration required to supply a plant depends on whether P uptake capacity is near its maximum, or not (Fig. 1). Increasing PUE has greatest effect when P uptake is near its maximum. In addition, PUE also reduces the P offtake from fields (whereas PAE does not). Reducing P input and the soil-available P concentration required for optimal crop production will have both economic and environmental benefits.

Significant progress has been made recently in enhancing PUE in plants, which involves numerous metabolic and transport processes, including Pi release from the vacuole, the liberation from organic P pools and P (re)distribution between cells

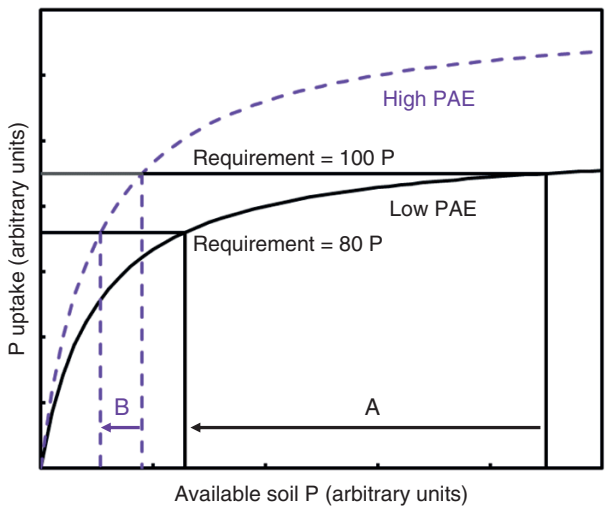

FIG. 1. Hypothetical relationships between available soil phosphorus (P) and P uptake by plants with low (black curve) and high (purple curve) P acquisition efficiency (PAE). The available soil P to supply plants with requirements of 100 P and 80 P, implying an increase in physiological P utilization efficiency (PUE) of 20 %, are shown. A and B indicate the reduction by increasing PUE in the available soil P concentration required by plants with low PAE and high PAE. Note that A is larger than B.

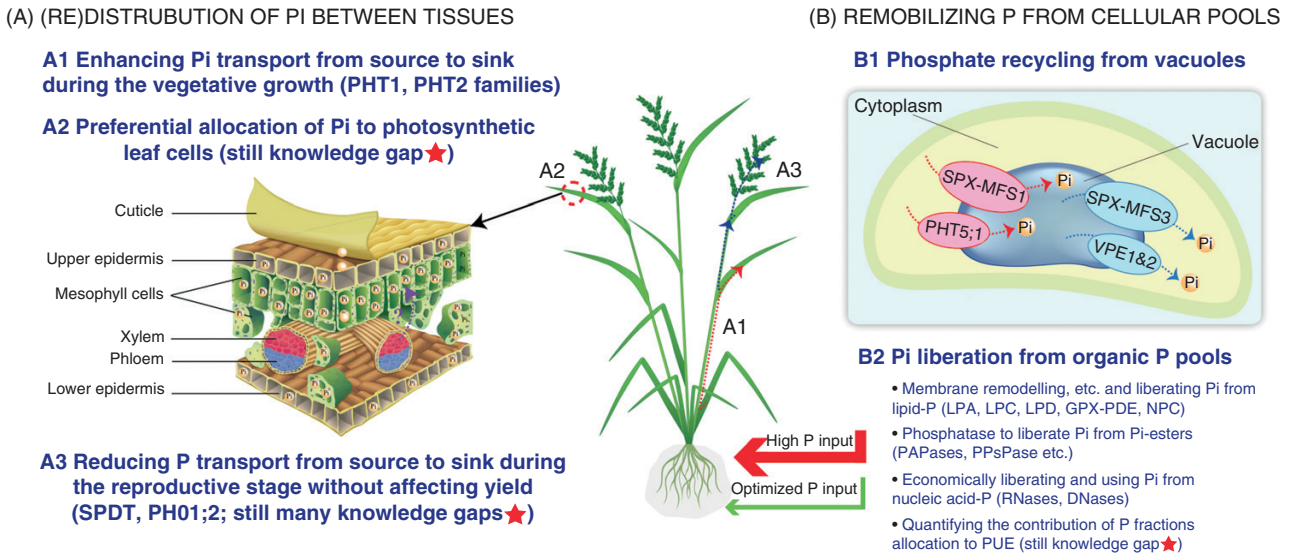

Fig. 2. Plant strategies to enhance phosphorus utilization efficiency. These strategies, which include Pi (re)distribution in tissues and cells (A), and Pi release from vacuoles and Pi liberation from organic P pools (B), will have implications for P recycling and utilization in crop production systems, leading to reduced P fertilizer requirements, enhanced nutritional quality of food and reduced P-related environmental pollution. Abbreviations: SPX-MFS, SYG1/PHO81/XPR1 domain and the major facilitator superfamily; PHT, phosphate transporter; VPE, vacuolar phosphate efflux transporter; PUE, phosphorus utilization efficiency; RNases, ribonucleases; DNases, deoxyribonucleases; PAPases, purple acid phosphatases; PPsPase, pyrophosphate-specific phosphatase; LPA, phospholipase A; LPC, phospholipase C; LPD, phospholipase D; GPX-PDE, glycerophosphodiester phosphodiesterases; NPC, non-specific phospholipase; SPDT, SULTR-like phosphorus distribution transporter; Pi, phosphate. The red and blue arrows represent the (re)distribution of Pi from senescent leaves to young leaves and from flag leaves to grains, respectively. The red asterisks indicate that there are still many knowledge gaps in improving PUE in plants.

and tissues (Fig. 2). Greater yields are achieved in plants that partition P more effectively to improve resource capture through photosynthesis and plant growth. In addition, it is suggested that plants with greater PUE would accumulate less P in seeds as phytate, thereby reducing P offtakes from fields and the P fertilizer input required for the next crop. Candidate genes have been identified (Table 2) that might enable marker-assisted breeding or genetic modification strategies to improve PUE in crops.

Several questions remain: (1) Does P remobilization alter the distribution of photosynthates or other nutrients? The former is unlikely unless altered P distribution affects sink strength and the latter is unlikely because nutrients are not transported in association with P in the phloem. However, manipulating Pi loading of the phloem might alter the fluxes of other anions or cations to the sink tissue because of the necessity for charge balance. (2) If seed P (and phytate) concentrations are reduced, will this affect crop production or human health? Here it has been argued that careful agronomy during germination and seedling establishment would offset a lack of P in the seed. In terms of human health, it has been argued that reducing phytate in seeds will improve the availability of cationic micronutrients to monogastric animals, although we acknowledge that phytate itself has been attributed some health benefits. (3) Are there strategies other than improving P metabolism and remobilization that might enhance PUE? For example, are there opportunities for manipulating phenology, plant architecture or symbiotic interactions? (4) Are any modifications to crop husbandry required to produce low-P crops? For example, will it be necessary to develop precision fertilizer strategies to enable the successful establishment of seedlings from low-P seed? Finally, (5) in addition to reducing environmental pollution by reducing soil P concentration upon improving PUE of crops, are there any other environmental consequences of tightening the Pi cycle in this way? For example, will it affect local vegetation, microbial or faunal communities?

In conclusion, improving PUE in crops would enable reductions in P fertilizer-inputs, in P-offtakes from land and in soil-available P concentration required for crop production. Several genetic strategies have been identified that could improve PUE by manipulating P metabolism and P redistribution within the plant. However, several questions still need to be addressed for this strategy to succeed. These relate, in particular, to the development of agronomy enabling the production of low-P crops, the viability of low-P seeds and the nutritional quality of low-P produce.

FUNDING

This work was supported financially by the National Science Foundation of China (Nos. 31972496, 31572190, 32130094) and the Deutsche Forschungsgemeinschaft (DFG) – 328017493/GRK 2366. P.J.W. was supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government.

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