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ORIGINAL ARTICLE

Soy and mustard effectively mobilize phosphorus from inorganic and organic sources

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Abstract We aimed to investigate phosphorus (P) mobilization by different plant species from organic and inorganic sources in relation to different P mobilization mechanisms. Knowledge about P mobilization is important for producing crops on P sources other than phosphate rock-derived fertilizers. We conducted a greenhouse experiment with four plant species (maize, soy, lupin, mustard) and three P sources ($FePO_4$, phytate, struvite). We determined pH and phosphomonoesterase activity in the rhizosphere using pH imaging and soil zymography. At harvest, root exudates were analyzed for phosphomonoesterase activity, pH, organic acids, and dissolved organic carbon (DOC). Plants were analyzed for biomass, root length, and P content. Struvite was more plant-available than phytate and $FePO_4$ as indicated by higher plant P contents. Soy had the highest biomass and P content, irrespective of P source. Soy exuded up to 12.5 times more organic acids and up to 4.2 times more DOC than the other plant species. Lupin had a 122.9 times higher phosphomonoesterase activity than the other plant species with phytate. The pH in the exudate solution of mustard was on average 0.8 pH units higher than of the other plant species. P uptake by mustard and soy seemed to have also benefited from large root lengths. Taken together, our study indicates that soy has a particularly high potential to mobilize P from struvite and phytate, while mustard has a high potential to mobilize P from $FePO_4$. Therefore, soy and mustard seem to be good options for agricultural production that relies less on phosphate rock-derived fertilizers.

Keywords Plant phosphorus mobilization · Struvite · Phytate · Iron phosphate · Organic acids · Phosphomonoesterase activity

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Introduction

Phosphorus (P) is essential for crop production since it is an integral constituent in the structural and cellular metabolism of plants as component of, e.g., adenosine triphosphate (ATP), nucleic acids, and phospholipids of biomembranes, and is thus involved

in transferring information (DNA, RNA) and energy (ATP, ADP) (Ashley et al. 2011; George et al. 2016; Marschner 2012). To increase crop yields and avoid P limitation, huge amounts of P fertilizers, i.e., about 46 million metric tons of P_2O_5 per year, mainly derived from phosphate rock, are applied globally in agricultural production (Cordell and White 2014; IFA 2022). However, the application of phosphate rock-derived fertilizer is increasingly problematic since phosphate rock represents a finite and geographically unevenly distributed resource (Ashley et al. 2011; George et al. 2016). Thus, there is a need to reduce the reliance on phosphate rock-derived fertilizers, for instance through cultivation of crops that effectively mobilize less easily available soil P forms and recycled P sources (George et al. 2016; Sulieman and Mühling 2021).

Plants have developed various mechanisms to mobilize P from different sources, which might be used to reduce the reliance on phosphate rock-derived fertilizers in agriculture. These mechanisms can be summarized as 'root foraging' via morphological adaptations and 'P mining' via physiological adaptations to P deficiency (Lyu et al. 2016; Richardson et al. 2011; Wen et al. 2021). Root foraging allows plants to acquire nutrients from a greater soil volume and minimizes the distance between roots and plant-available orthophosphate anions in soil by extending the root system and increasing the root surface (Ma et al. 2018; Richardson et al. 2011; Wen et al. 2019). Especially *Brassicaceae* exhibit a ramified root system with thin, long, and intensively branched roots, whereas *Lupinus* species form thick and comparatively short taproots (Lyu et al. 2016; Wen et al. 2019). In contrast to root foraging, P mining refers to the mobilization of phosphate anions from sparingly soluble P sources by exuding various substances, such as phosphatases and low molecular weight organic acid anions (LMWOA), into the soil (Richardson et al. 2011; Wen et al. 2021).

Up to 80% of soil P is present as organic P in the topsoil, of which the majority (60–90%) exists as orthophosphate monoesters, with *myo*-inositol hexakisphosphate (phytate) being the most abundant form (Dalal 1977; Liu et al. 2022; Turner et al. 2002). Mobilizing P from phytate involves two steps: organic P needs to be released from precipitates and adsorption sites before it can be mineralized through hydrolysis of the ester bonds via extracellular phosphomonoesterase enzymes, namely phytases (Liu et al. 2022; Menezes-Blackburn et al. 2018; Richardson et al. 2009). However, a part of the organic soil P pool and particularly phytate is stabilized against mineralization by adsorption to mineral surfaces and is therefore only slowly hydrolyzed by enzymes (Jarosch et al. 2015; Menezes-Blackburn et al. 2018; Nannipieri et al. 2011). Moreover, plant species differ considerably in their capacity to exude phosphomonoesterases including phytases. Legumes, and particularly *Lupinus* species, are known for a high phosphomonoesterase activity in the rhizosphere, thus likely mobilizing organic P more effectively than *Gramineae* and *Brassicaceae* (Sulieman and Mühling 2021; Wen et al. 2019). However, the amount of released phytases differ among different legumes, both in absolute terms and relative to other phosphatases (Dong et al. 2020; Gilbert et al. 1999; Tang et al. 2021).

Orthophosphate anions have a high affinity for metal cations, e.g., of iron (Fe^{2+} and Fe^{3+}), with which they precipitate, forming sparingly soluble P minerals such as iron phosphate ($FePO_4$) (Chang and Jackson 1958; Richardson et al. 2009). $FePO_4$ is also formed during wastewater treatment and its use in agriculture as a fertilizer can thus increase P recycling (Li et al. 2020b; Wilfert et al. 2015). Mobilizing P from $FePO_4$ requires changes in the precipitation-dissolution equilibrium, which can be achieved by increases in the soil pH (Hinsinger 2001; Lindsay 1979; Richardson et al. 2009). Plants can modify the rhizosphere pH by releasing protons or hydroxyl ions and/or by exuding LMWOA. The latter can also mobilize inorganic P by modifying the surface characteristics of soil colloids, by successfully competing with phosphate for sorption sites, or by chelating cations bound to P (Hinsinger et al. 2003; Richardson et al. 2009; Wang and Lambers 2020). However, only some plant species exude LMWOA at high rates or change the rhizosphere pH substantially. Legumes, and particularly *Lupinus* species, are known for a high LMWOA exudation (Wang and Lambers 2020; Wen et al. 2019), while different *Brassicaceae* have been shown to substantially alkalize their rhizosphere, thus increasing P mobilization from $FePO_4$ (Marschner et al. 2007). However, former research has also shown that LMWOA exudation is not necessarily strongly aligned with a plant species' capacity to mobilize P from $FePO_4$ (Pearse et al. 2007).

Struvite (ammonium magnesium phosphate; NH_4MgPO_4) is frequently formed as a byproduct of wastewater and sludge treatment (Kataki et al. 2016; Talboys et al. 2016). Compared to other recycling products, struvite has a high P content, contains also N, and tends to have a low concentration of heavy metals and other contaminants (Faucon et al. 2015; Schneider et al. 2019). Yet, the capacities of different plant species to mobilize P from struvite are still not fully understood. Lupin and buckwheat have been shown to mobilize P from struvite through the exudation of LMWOA (Robles-Aguilar et al. 2019; Talboys et al. 2016). Moreover, lupin has been shown to be more efficient in P uptake from struvite than maize due to rhizosphere acidification (Robles-Aguilar et al. 2020). However, the capacities of several other common crop species to mobilize P from struvite have not yet been investigated.

Our study aimed to investigate the mechanisms of plant P mobilization from different P sources in relation to plant P uptake by different plant species in order to identify plant species that effectively use P sources other than phosphate rock-derived fertilizers. For this purpose, we conducted a greenhouse experiment with three different P sources (phytate, $FePO_4$, and struvite) that require different P mobilization mechanisms and four different plant species (maize, soy, lupin, and mustard) that likely have contrasting mechanisms of P mobilization. We hypothesized that (i) plant species with a high LMWOA exudation effectively mobilize P from struvite and $FePO_4$, (ii) rhizosphere alkalinization mobilizes P from $FePO_4$, and (iii) plant species with a high phosphomonoesterase activity in the rhizosphere effectively mobilize P from phytate. To test these hypotheses, we analyzed the spatial distribution of rhizosphere pH and phosphomonoesterase activities during plant growth using the *in situ* techniques pH imaging and soil zymography. Additionally, we collected root exudates at harvest, in which pH, phosphomonoesterase activity, LMWOA, and dissolved organic carbon (DOC) were measured, before plants were analyzed for biomass production, P content, and root length.

Materials and methods

Experimental setup

We conducted a greenhouse experiment with four plant species grown in rhizoboxes in a mineral substrate with three different P sources. The mineral substrate consisted of 20% (vol.) perlite and 80% (vol.) quartz sand, from which 50% (wt.) had a grain size of 0.1–0.4 mm and 50% (wt.) had a grain size of 0.7–1.2 mm. A mix of micronutrients (RADIGEN® Micronutrient mixed fertilizer, Terraflor GmbH, Iserlohn, Germany) was added to the mineral substrate (320 mg rhizobox^{-1}), containing 5.0% MgO, 2.0% Fe, 1.5% Cu, 1.0% Mn, 0.8% Mo, 0.6% B, and 0.5% Zn. One of the following P sources was added to the mineral substrate (150 mg P rhizobox^{-1}): iron phosphate (iron(III) phosphate dihydrate: $FePO_4 \times 2H_2O$; Sigma-Aldrich, Merck KGaA, Darmstadt, Germany), phytate (phytic acid sodium salt hydrate: $C_6H_{18}O_{24}P_6 \times xNa^+ \times yH_2O$; Sigma-Aldrich), and struvite (ammonium magnesium phosphate hydrate: $NH_4MgPO_4 \times xH_2O$; Sigma-Aldrich). Further nutrients were supplied with a P-free nutrient solution as described below. The mineral substrate was filled into the rhizoboxes to a final bulk density of 1.1 g cm^{-3}, which equals 1.7 kg of mineral substrate (dry weight) per rhizobox. Rhizoboxes were made of PVC and had an inner size of 39.2 × 19.2 × 2.2 cm (h × w × d).

In each rhizobox, one out of four plant species was sown: maize (*Zea mays* L. cv. Golden Bantam, Bingenheimer Saatgut AG, Echzell, Germany), soy (*Glycine max* (L.) Merr. cv. Lica, Marktgesellschaft der Naturland Bauern AG, Hohenkammer, Germany), blue lupin (*Lupinus angustifolius* L. cv. Rumba, Templiner Kräutergarten, Templin, Germany), and white mustard (*Sinapis alba* L., Bingenheimer Saatgut AG). All seeds except for mustard were soaked in water for 24 h before seeds of a consistent size were sown at a rate of one seed per rhizobox. All treatments were replicated four times summing up to a total number of 48 rhizoboxes (four plant species × three P sources × four replicates). However, one rhizobox of lupin supplied with struvite failed shortly before harvest. The plants were sown in August 2019 and harvested after 10 weeks in October 2019.

An inoculum was applied to the mineral substrate at the beginning of the experiment in order to introduce a soil microbial community. For this purpose, fresh soil with a loamy sandy texture was sampled from an agricultural soil cultivated with the same plant species used here. In the field, soy and lupin seeds had been inoculated with commercial *Bradyrhizobium* sp. inoculants, which are assumed to be also part of the microbial community introduced

here (for details, see Schwerdtner and Spohn 2021). The soil was sieved (< 2 mm), mixed with tap water (1:2), and shaken on an overhead shaker for 1 h before being filtered through cellulose filters (Rotilabo®, type 113P, Carl Roth GmbH & Co. KG, Karlsruhe, Germany). The filtrate was mixed with tap water to a final soil:water ratio of 1:4 and stored at 20 °C over night before being applied to all rhizoboxes. The final soil inoculum had the following chemical properties (l^{-1} inoculum): 15.3 mg organic C, 4.4 mg N, 0.9 mg P, and pH 7.9. Each rhizobox received 180 ml of soil inoculum and 50 ml of tap water to adjust the mineral substrate to 75% water holding capacity (WHC).

The rhizoboxes were placed in an open greenhouse at the University of Bayreuth under ambient conditions and without artificial light. The rhizoboxes were placed in a randomized block design on a wooden rack that kept them inclined by 50° throughout the experiment, and they were rearranged randomly after 5 weeks. The inclination of the rhizoboxes made the roots grow along the bottom wall of the rhizoboxes, which made it possible to conduct imaging analyses (see below) and to remove the entire plant at harvest with very limited damage to the root system. Rhizoboxes were watered every two days with tap water to 75% WHC as measured by weight. In addition, a P-free nutrient solution was applied regularly. For this purpose, an adapted Ruakura solution (Smith et al. 1983) was used, where KH_2PO_4 was substituted by KNO_3 and K_2HPO_4 by K_2SO_4. The final nutrient solution applied to the rhizoboxes contained (l^{-1}): 220 mg $Mg(NO_3)_2 \times 6\ H_2O$, 746 mg $Ca(NO_3)_2 \times 4\ H_2O$, 377 mg NH_4NO_3, 189 mg KNO_3, 367 mg K_2SO_4, 27 mg Na_2SO_4, and 15 mg NaCl. In total, 9.2 mg N kg^{-1} substrate were applied in the form of inoculum and nutrient solution.

Six weeks after plant emergence, pH imaging and soil zymography were performed to determine the spatial distribution of pH and phosphomonoesterase activity (see below). At harvest, 70 days after plant emergence, root exudates were collected, and plants were analyzed for biomass production, root length, and P concentrations (see below).

pH imaging

The distribution of pH in the rhizosphere was analyzed *in situ* by pH imaging, following Marschner and Römheld (1983) with modifications. The pH indicator bromocresol purple (Sigma-Aldrich) was dissolved in deionized water (0.6%). NaOH was added dropwise for better dissolution as described by Nkebiwe et al. (2016). The day before analysis, a boiled agar solution (1.3% agarose; Sigma-Aldrich) was mixed with the pH indicator solution (final pH indicator concentration of 0.006%), adjusted to mineral substrate pH with NaOH, and cast in glass systems usually used for gel electrophoresis with an inner size of 24.5 × 18.5 × 0.1 cm. Gels were plastic-wrapped to prevent drying and stored overnight at 20 °C to allow acclimatization. Rhizoboxes were transferred to the 20 °C climate chamber 1 h before analyses to allow acclimatization of the mineral substrate. The pH indicator gels were cut into three pieces, each with a size of 8 × 18 cm. Each gel was attached to the soil surface of one rhizobox to a soil depth of 18 cm (from the top, box-centered) and covered with a plastic sheet. After 12 min of incubation in the dark at 20 °C, gels were photographed with a digital camera (EOS 1100D, Canon). No quantitative image analysis was performed since the mineral substrate gave no uniform background values due to the mixing with perlite. Instead, representative pH images of each plant species supplied with one of the three P sources are presented in Fig. S1 (Supplement). Photos of the root systems are not included in the study as it was practically impossible to photograph the roots accordingly since mineral substrate and roots had very similar colors.

Soil zymography

Directly after pH imaging, the distribution of phosphomonoesterase activity was measured *in situ* by soil zymography following Spohn and Kuzyakov (2013) with modifications. No agarose gels were used as in Holz et al. (2019) as we used a mineral substrate and thus the gel, which is thought to protect the membrane from staining with organic material, was not required. The substrate 4-methylumbelliferyl phosphate (Sigma-Aldrich) was dissolved in deionized water to a concentration of 2 mM. Membrane filters of nylon (0.45 µm pore size; Nantong FilterBio Membrane Co. Ltd., Jiangsu, China) with a size of 8 × 31 cm were coated with this solution. The membranes were allowed to dry flat for 1 min at room temperature (20 °C) on aluminum foil, before being attached to the soil surface of one rhizobox to a soil

depth of 31 cm (from the top, box-centered). After 30 min of incubation at 20 °C in the dark, the membrane was removed from the soil surface, cut into two equal pieces, and each piece was photographed with a digital camera (D60, Nikon) on an epi-UV-desk (Desaga, Heidelberg, Germany) at 366 nm wavelength. The cutting was done to ensure equal distribution of UV light all over the zymogram.

For calibration, membranes were soaked in 4-methylumbelliferone (MUF; Sigma-Aldrich) of different concentrations (0, 25, 75, 125, 200 µM). The membranes were also allowed to dry for 1 min and then photographed as described for the zymograms. Phosphomonoesterase activity was calculated based on a linear correlation between the different MUF concentrations and the corresponding gray values of the images (Spohn and Kuzyakov 2013).

The zymograms were analyzed using the open-source software ImageJ (version 1.52a; Rasband 2018). For this purpose, the photographs were converted into 8-bit, i.e., grayscale images, and a digital grid with cells of 10×10 pixels was laid on the images, similar as in Hofmann et al. (2016). The mean gray value of each grid cell was determined, and the twenty highest gray values of each rhizobox (considering both pieces of the zymogram) were arithmetically averaged to obtain one average value per rhizobox, i.e., per plant. The corresponding phosphomonoesterase activities were calculated based on the calibration line and the incubation time. Representative zymograms of each plant species supplied with phytate are presented in Fig. S2 (Supplement).

Root exudate collection

Root exudates were collected in sterile deionized water using the soil-hydroponic-hybrid sampling approach (Oburger and Jones 2018). For this purpose, the bottom walls of the rhizoboxes were opened at harvest and plants were removed as carefully as possible to prevent root damage. Roots were gently shaken and washed with deionized water to remove adhering substrate particles and potential metabolites (Oburger and Jones 2018). The entire root system of the intact plant was then transferred to a sterile beaker that was filled with a known volume of sterile deionized water (between 50 and 125 ml) so that roots were completely submerged. We used sterile deionized water instead of a $CaCl_2$ solution since this reduces the background matrix for the analyses while not altering exudation patterns (Egle et al. 2003; Oburger and Jones 2018). Plants in beakers were stored at 20 °C in a climate chamber with artificial lighting (650 µmol m^{-2} s^{-1}). After 4 h, plants were removed, and beakers were swayed to homogenize the exudates in the solution. The exudate solutions were filtered through 0.2 µm syringe filters and four aliquots were frozen for subsequent analyses of pH, phosphomonoesterase activity, LMWOA, and DOC. All plants were sampled in a way ensuring that exudate collection took place during peak metabolic activity, i.e., collection started 3.5 ± 1 h after sunrise, as recommended in Oburger and Jones (2018). Since we used a relatively short exudate collection period and maintained very similar temperatures during plant growth and exudate collection, we assume that plant metabolism and therefore exudation patterns do not differ between growth and sampling conditions (Oburger and Jones 2018).

Biomass analyses

After the plants were removed from the exudate collection beakers, aboveground biomass (AGB) was separated from belowground biomass (BGB). AGB was immediately dried at 60 °C for 24 h, then weighed and milled. The BGB was washed again with deionized water and stored over night at 2 °C. For root length determination, two plant individuals per species and P source (24 individuals in total) were chosen (due to time constraints during harvest). The root length was determined using a flatbed scanner (Epson Perfection V700, Seiko Epson Corporation, Nagano, Japan) and the software WinRhizo™ 2008 (Regent Instruments Inc., Québec, Canada). The BGB was submerged in a water bath, neatly arranged to avoid root overlapping, and scanned at 400 dpi resolution. After root length analysis, BGB of all plants was dried at 60 °C, weighed, and milled.

The biomass samples (AGB and BGB of each plant) were analyzed for total P concentrations after pressure digestion in concentrated nitric acid using inductively coupled plasma-optical emission spectroscopy (Vista-Pro radial, Varian Inc., Palo Alto, USA).

Exudate analyses

pH The pH in the exudate solution was measured with a pH electrode (WTW SenTix 51, Xylem Analytics GmbH & Co. KG, Weilheim, Germany).

Phosphomonoesterase activity Phosphomonoesterase activity in the exudate solution was measured using the fluorogenic substrate 4-methylumbelliferyl phosphate following Marx et al. (2001), German et al. (2011), and Herold et al. (2014). In brief, the exudate samples (50 µl) were pipetted into black polystyrene 96-well microplates (BRANDplates®, Brand GmbH & Co. KG, Wertheim, Germany) having four replicates. Sterile deionized water (50 µl) and substrate solution (100 µl) were added. Microplates were covered and pre-incubated in the dark at 15 °C for 30 min and measured fluorometrically after 0, 60, and 180 min with 360 nm excitation and 460 nm emission filters (Herold et al. 2014) by a microplate reader (Infinite® 200 PRO, Tecan Trading AG, Männedorf, Switzerland). Between measurements, microplates were incubated in the dark at 15 °C. Enzyme activities were calculated according to German et al. (2011) modified by Widdig et al. (2019). Fluorescence values were corrected for quenching, sample fluorescence, and substrate fluorescence.

LMWOA LMWOA were analyzed using high-performance liquid chromatography-mass spectrometry (HPLC–MS). For this purpose, the exudate samples were loaded on a HPLC RP-C18 column (Luna Omega 1.6 µm PS C18, 100 Å, 100 × 2.1 mm, Phenomenex Inc., Torrance, USA; operated as part of an Ultimate 3000 HPLC, Thermo Fisher Scientific GmbH, Bremen, Germany), which was connected to a Q Exactive mass spectrometer (Thermo Fisher Scientific GmbH) equipped with a hybrid quadrupole orbitrap mass analyzer (maximum mass range 50–6000 Da, resolution 140.000 @ m/z = 200). A 10 min isocratic elution with pure water (HPLC-grade, spiked with 0.2% formic acid) at a flow rate of 0.3 ml min^{-1} was applied. Mass spectra were acquired after electrospray ionization (ESI negative) in full scan mode ($50 < m/z < 750$) recording the total ion current. For evaluation (i.e., identification and integration/quantitation) of the LMWOA, their characteristic mass traces were used (Table S1; Supplement).

DOC Dissolved organic carbon (DOC) was analyzed using a Total Carbon Analyzer (TOC-TN Analyzer, multi N/C 2100, Analytik Jena GmbH, Jena, Germany).

Calculations

The total biomass (TBM) was calculated as the sum of the dry weights (DW) of AGB and BGB for each plant. The plant P concentration (in mg P g^{-1} DW) was calculated based on the P concentrations of AGB and BGB and the DW of AGB and BGB for each plant. The plant P content (in mg P $plant^{-1}$) was calculated as the sum of AGB and BGB P content (calculated by multiplying the P concentrations of AGB and BGB with the DW of AGB and BGB, respectively).

The pH in the exudate solution was converted into the H^+ concentration, and subsequently the H^+ concentration was multiplied by the volume of sterile deionized water and reconverted into pH in order to correct for the different volumes. The phosphomonoesterase activity and DOC concentration in the exudate solution were multiplied by the volume of sterile deionized water, in which roots were submerged in order to correct for the different volumes and gain results per plant.

The exudation of each LMWOA (in µmol $plant^{-1}$) was calculated by multiplying the LMWOA concentrations in the exudate solution (in mg l^{-1}) with the volume of sterile deionized water and dividing by the molar mass of the respective LMWOA. The concentration of each LMWOA (in µmol $plant^{-1}$) was multiplied with the number of carboxyl groups (1, 2, or 3, respectively; Table S1; Supplement), and all numbers were totaled up to calculate the total number of carboxyl groups in the exudate solution. The carboxyl groups (in µmol $plant^{-1}$) were divided by the BGB DW in order to gain results per g root DW. For two plant individuals per treatment, the carboxyl groups (in µmol $plant^{-1}$) were also divided by the root length in order to gain results per cm root length.

Statistical analyses

Data were tested for significant differences both among plant species (tested separately for each P source) and among P sources (tested separately for each plant species). Prior to all statistical analyses, normality was checked with Shapiro–Wilk normality

tests, and homogeneity of variances was tested with Levene's tests. Where normality and homogeneity assumptions were met, analyses of variance followed by Tukey's post-hoc tests were conducted to identify significant differences. Where normality and homogeneity assumptions were not met, Kruskal–Wallis tests followed by post-hoc tests using the criterium Fisher's least significant difference and Holm correction for p adjustment were conducted to identify significant differences. All statistical analyses were performed in R (version 3.5.2; R Core Team 2018) using the packages agricolae (version 1.3–2; Mendiburu 2020), car (version 3.0–7; Fox and Weisberg 2019), dplyr (version 0.8.5; Wickham et al. 2020), and ggplot2 (version 3.3.0; Wickham 2016). Data on root length were not tested for significant differences since the sample size was too low (n = 2).

Results

Biomass production

AGB was 870 ± 353 mg plant^{-1} and BGB was 244 ± 104 mg plant^{-1}, averaged across all plant species and P sources (Table 1). When P was provided in the form of phytate, TBM of soy was highest and was significantly higher, by a factor of 2.5, than TBM of lupin ($p = 0.005$; Table 1). When P was provided in the form of struvite, TBM of soy was also highest, and TBM of soy and mustard were significantly higher than of lupin and maize ($p \leq 0.007$; Table 1). When P was provided in the form of $FePO_4$, no significant difference in TBM among the plant species was found (Table 1).

Root length of soy, and to a lesser extent of mustard, tended to be larger than of maize and lupin, especially when supplied with phytate or struvite (Fig. S3; Supplement). Irrespective of the P source, mustard and soy had a thin and intensively branched root system that already filled the whole rhizobox 6 weeks after plant emergence. Maize had thicker roots that penetrated almost exclusively the upper third of the substrate in the rhizoboxes, whereas lupin formed thick tap roots that reached the bottom of the rhizoboxes but did not fill the whole volume of the rhizoboxes 6 weeks after plant emergence.

Plant phosphorus

Plant P concentrations (in mg g^{-1}) differed significantly among all plant species and decreased in the order mustard > lupin > soy > maize when P was provided in the form of $FePO_4$ ($p < 0.003$; Table 1). More precisely, plant P concentration of mustard was significantly higher, by a factor of 2.8, compared to maize ($p < 0.001$; Table 1). When P was provided in the form of phytate, plant P concentrations

Table 1 Aboveground (AGB), belowground (BGB), and total biomass (TBM) as well as plant P concentrations of maize, soy, lupin, and mustard grown with three different P sources

Species	P source	AGB (mg plant^{-1})	BGB (mg plant^{-1})	TBM (mg plant^{-1})	Plant P (mg g^{-1})
Maize	$FePO_4$	889.3 ± 397.3	234.8 ± 122.5	1124.0 ± 510.7	1.11 ± 0.13^{dB}
	Phytate	962.4 ± 370.7^{a}	281.8 ± 152.1	1244.1 ± 521.9^{ab}	1.00 ± 0.17^{cB}
	Struvite	674.6 ± 73.1^{b}	203.5 ± 68.2	878.1 ± 122.2^{b}	1.71 ± 0.18^{bA}
Soy	$FePO_4$	1017.4 ± 487.1	273.4 ± 147.7	1290.8 ± 630.7	1.77 ± 0.37^{cB}
	Phytate	1389.6 ± 477.0^{a}	365.4 ± 106.8	1755.0 ± 581.3^{a}	2.29 ± 0.38^{aB}
	Struvite	1211.6 ± 74.1^{a}	290.6 ± 71.9	1502.3 ± 140.2^{a}	4.51 ± 0.43^{aA}
Lupin	$FePO_4$	606.1 ± 176.6	239.0 ± 186.9	845.1 ± 350.5	2.40 ± 0.09^{bB}
	Phytate	495.1 ± 140.7^{b}	211.3 ± 58.1	706.4 ± 197.2^{b}	1.42 ± 0.11^{bC}
	Struvite	636.7 ± 77.1^{b}	180.0 ± 64.8	816.7 ± 140.2^{b}	4.37 ± 0.31^{abA}
Mustard	$FePO_4$	699.8 ± 187.4^{B}	186.0 ± 27.8^{B}	885.8 ± 210.1^{B}	3.13 ± 0.38^{aAB}
	Phytate	785.9 ± 70.6^{abAB}	193.0 ± 19.0^{AB}	978.9 ± 66.1^{abAB}	2.55 ± 0.34^{aB}
	Struvite	1011.5 ± 154.6^{aA}	250.8 ± 43.1^{A}	1262.3 ± 121.0^{aA}	4.18 ± 1.02^{abA}

Numbers show means ± standard deviations. Different lowercase letters indicate significant differences ($p < 0.05$) among the plant species, tested separately for each P source. Different capital letters indicate significant differences among the P sources, tested separately for each plant species. Absence of letters indicates that there was no significant difference

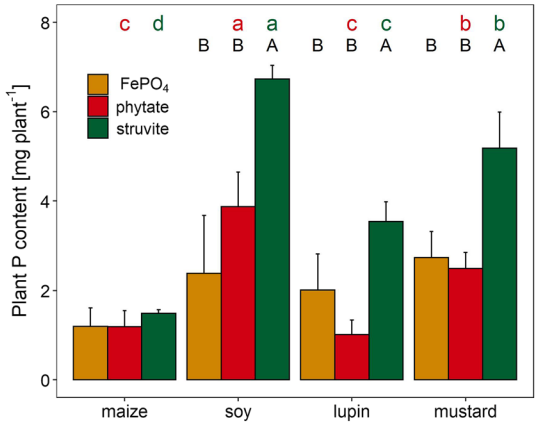

Fig. 1 Plant P content of the total biomass which is the sum of P in AGB and BGB. Columns show means and error bars indicate standard deviations. Different lowercase letters indicate significant differences ($p < 0.05$) among the plant species, tested separately for each P source. Different capital letters indicate significant differences among the P sources, tested separately for each plant species. Absence of letters indicates that there was no significant difference

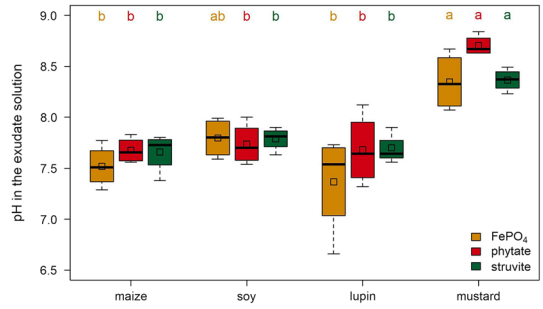

Fig. 2 pH in the exudate solution. Squares show means. Different lowercase letters indicate significant differences ($p < 0.05$) among the plant species, tested separately for each P source. No significant difference was found among the P sources, tested separately for each plant species

of mustard and soy were significantly higher than of maize ($p < 0.001$) and lupin ($p \leq 0.009$; Table 1). When P was provided in the form of struvite, plant P concentrations of soy ($p = 0.028$), lupin ($p = 0.052$), and mustard ($p = 0.052$) were higher, by a factor of 2.4 to 2.6, than those of maize (Table 1). Lupin was the only plant species for which the P concentration was significantly higher when supplied with $FePO_4$ than when supplied with phytate ($p < 0.001$; Table 1).

Plant P content (in mg plant^{-1}) of soy was significantly higher, by a factor of 3.8, 3.3, and 1.6, respectively, than of lupin ($p < 0.001$), maize ($p < 0.001$), and mustard ($p = 0.009$) when P was provided in the form of phytate. Moreover, plant P content of mustard was significantly higher, by a factor of 2.5 and 2.1, respectively, than of lupin ($p = 0.005$) and maize ($p = 0.013$) when P was provided in the form of phytate (Fig. 1). When P was provided in the form of struvite, plant P contents significantly differed among all plant species and decreased in the order soy > mustard > lupin > maize ($p < 0.007$). More precisely, plant P content of soy was significantly higher, by a factor of 4.5, than of maize ($p < 0.001$; Fig. 1). When P was provided in the form of $FePO_4$, no significant difference in plant P content was found among the plant species. Plant P contents of soy, lupin, and mustard were significantly higher when supplied with struvite than when supplied with phytate ($p < 0.004$) and $FePO_4$ ($p \leq 0.020$). Soy was the only plant species for which the plant P content was slightly higher with phytate than $FePO_4$ ($p = 0.097$; Fig. 1). The P contents of all plant species were higher in AGB than in BGB (Table S2; Supplement).

Exudate pH and rhizosphere pH

The pH in the exudate solution of mustard was 0.8 pH units higher than in the exudate solution of the other plant species, when averaged across P sources (Fig. 2). When P was provided in the form of phytate or struvite, the pH in the exudate solution of mustard was significantly higher, by 1.0 and 0.7 pH units, respectively, than the pH of all other plant species ($p \leq 0.001$; Fig. 2). When P was provided in the form of $FePO_4$, the pH in the exudate solution of mustard was significantly higher, by 1.0 and 0.8 pH units, respectively, than of lupin ($p = 0.004$) and maize ($p = 0.014$), and it tended to be higher than of soy ($p = 0.117$; Fig. 2). The pH in the exudate solution of mustard was slightly higher when supplied with phytate than when supplied with $FePO_4$ ($p = 0.061$) or struvite ($p = 0.060$; Fig. 2).

In addition, the pH images, taken 6 weeks after plant emergence, revealed a comparatively strong rhizosphere acidification by maize and an intermediate rhizosphere acidification by soy, irrespective of the P source (Fig. S1; Supplement).

Phosphomonoesterase activity

When P was provided in the form of phytate, phosphomonoesterase activity of lupin was significantly higher, by a factor of on average 122.9, compared to the other plant species ($p < 0.022$; Fig. 3). When P was provided in the form of $FePO_4$, phosphomonoesterase activity of lupin was significantly higher, by a factor of 33.8, compared to soy and mustard ($p \leq 0.011$), and slightly higher than of maize ($p = 0.084$; Fig. 3). When P was provided in the form of struvite, phosphomonoesterase activity of lupin was also significantly higher, by a factor of 8.5, compared to the other plant species ($p < 0.001$; Fig. 3).

Soil zymography, conducted 6 weeks after plant emergence, revealed that lupin and soy had similarly high maximum phosphomonoesterase activities in the rhizosphere (Figs. S2 and S4; Supplement). When P was provided in the form of phytate, the phosphomonoesterase activities of lupin and soy were higher, by a factor of on average 1.8, compared to mustard ($p < 0.001$ and $p = 0.005$, respectively) and maize ($p = 0.002$ and $p = 0.126$, respectively; Fig. S4; Supplement).

Exudation of LMWOA

When P was provided in the form of struvite, the exudation of carboxyl groups by soy was significantly higher, by a factor of 12.5 and 7.3, respectively, compared to mustard ($p < 0.001$) and maize ($p = 0.002$), and slightly higher than of lupin ($p = 0.061$; Fig. 4). When P was provided in the form of $FePO_4$, the exudation of carboxyl groups by soy was significantly higher, by a factor of 10.1 and 3.3, respectively, compared to mustard ($p = 0.003$) and lupin ($p = 0.019$; Fig. 4). When P was provided in the form of phytate, the exudation of carboxyl groups by lupin was significantly higher, by a factor of 17.5 and 4.2, respectively, compared to mustard ($p < 0.001$) and maize

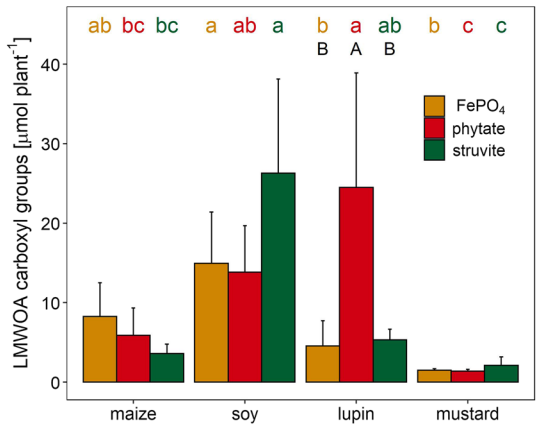

Fig. 4 Total number of LMWOA carboxyl groups in the exudate solution. Columns show means and error bars indicate standard deviations. Different lowercase letters indicate significant differences ($p < 0.05$) among the plant species, tested separately for each P source. Different capital letters indicate significant differences among the P sources, tested separately for each plant species. Absence of letters indicates that there was no significant difference

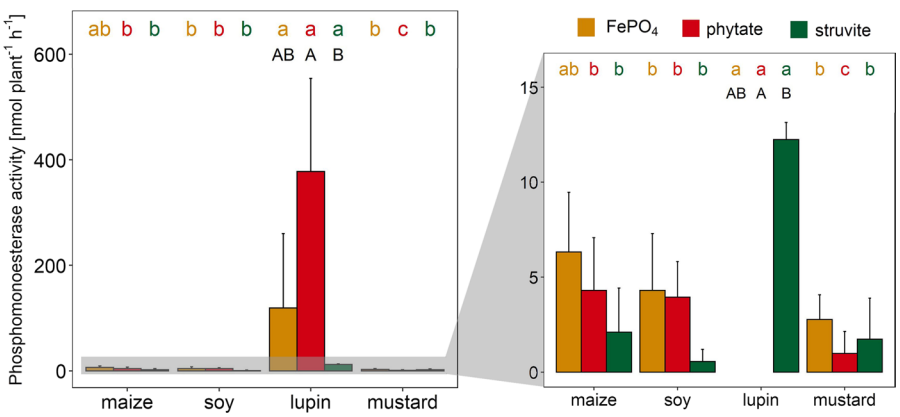

Fig. 3 Phosphomonoesterase activity in the exudate solution, including a zoom onto low values (right). Columns show means and error bars indicate standard deviations. Different lowercase letters indicate significant differences ($p < 0.05$) among the plant species, tested separately for each P source. Different capital letters indicate significant differences among the P sources, tested separately for each plant species. Absence of letters indicates that there was no significant difference

($p=0.011$), while LMWOA exudation did not differ significantly among lupin and soy ($p=0.253$; Fig. 4). Moreover, lupin exuded significantly more carboxyl groups when supplied with phytate than when supplied with $FePO_4$ ($p=0.008$) or struvite ($p=0.024$; Fig. 4). Similar findings were obtained when LMWOA data were normalized to BGB DW (Fig. S5a; Supplement). In contrast, maize, soy, and lupin exuded similar amounts of carboxyl groups per cm root length, which tended to be higher than of mustard, when P was provided in the form of struvite or $FePO_4$. When P was provided in the form of phytate, lupin tended to exude substantially more carboxyl groups per cm root length than the other plant species (Fig. S5b; Supplement).

Irrespective of P source, maize exuded mainly aconitate, followed by citrate and malate. Soy exuded mainly malonate, followed by citrate and malate. Lupin exuded mainly citrate, followed by malate. Mustard exuded mainly malate, followed by citrate. Succinate, fumarate, and gluconate played a minor role in all plant species (Table 2).

DOC exudation

When P was provided in the form of phytate, DOC exudation of soy was significantly higher, by a factor of 3.1, 2.4, and 2.0, respectively, than of mustard, maize, and lupin ($p<0.001$; Table 2). When P was provided in the form of struvite, DOC exudation of soy was significantly higher, by a factor of 3.2, than DOC exudation of maize ($p=0.009$), and slightly higher than DOC exudation of lupin and mustard ($p=0.052$; Table 2). When P was provided in the form of $FePO_4$, DOC exudation of soy was slightly higher than of mustard ($p=0.056$; Table 2).

Discussion

In the present study, we found indications that soy had a particularly high potential to mobilize P from struvite and phytate, while mustard had a high potential to mobilize P from $FePO_4$. The underlying mechanisms of plant P mobilization from the different P sources are discussed in the following.

Soy effectively mobilized P from struvite likely through LMWOA exudation

Our finding that soy had the highest P content of all investigated plant species when supplied with struvite (Fig. 1) is in accordance with a recent study showing that soy mobilized P from struvite nearly as effectively as from the highly soluble triple superphosphate and more effectively than wheat

Table 2 Gluconate (Glu), malate (Mal), malonate (Mao), succinate (Suc), fumarate (Fum), citrate (Cit), and aconitate (Aco) as well as dissolved organic carbon (DOC) in the exudate solution

Species	P source	Glu (µmol plant^{-1})	Mal (µmol plant^{-1})	Mao (µmol plant^{-1})	Suc (µmol plant^{-1})	Fum (µmol plant^{-1})	Cit (µmol plant^{-1})	Aco (µmol plant^{-1})	DOC (mg plant^{-1})
Maize	$FePO_4$	0.03 ± 0.01^{b}	0.32 ± 0.19^{b}	0.05 ± 0.01^{c}	0.04 ± 0.01	0.00 ± 0.00^{b}	0.26 ± 0.14^{b}	2.212 ± 1.218^{a}	0.77 ± 0.39
	Phytate	0.04 ± 0.02^{b}	0.34 ± 0.18^{b}	0.06 ± 0.01^{b}	0.05 ± 0.01	0.00 ± 0.00^{b}	0.44 ± 0.33^{c}	1.215 ± 0.686^{a}	0.70 ± 0.34^{b}
	Struvite	0.02 ± 0.01^{b}	0.26 ± 0.06^{c}	0.05 ± 0.01^{b}	0.04 ± 0.01	0.00 ± 0.00^{b}	0.34 ± 0.09^{c}	0.615 ± 0.420^{a}	0.44 ± 0.14^{b}
Soy	$FePO_4$	0.14 ± 0.07^{a}	2.19 ± 0.90^{a}	3.34 ± 1.77^{a}	0.06 ± 0.00	0.03 ± 0.02^{a}	1.19 ± 0.78^{a}	0.000 ± 0.000^{b}	1.77 ± 0.89
	Phytate	0.20 ± 0.05^{a}	1.49 ± 0.57^{a}	2.70 ± 1.31^{a}	0.06 ± 0.02	0.03 ± 0.01^{a}	1.69 ± 1.19^{b}	0.000 ± 0.000^{c}	1.68 ± 0.18^{a}
	Struvite	0.12 ± 0.05^{a}	2.58 ± 0.90^{a}	5.17 ± 3.09^{a}	0.06 ± 0.01	0.02 ± 0.00^{a}	3.50 ± 1.51^{a}	0.000 ± 0.000^{b}	1.43 ± 0.45^{a}
Lupin	$FePO_4$	0.04 ± 0.02^{ab}	0.60 ± 0.67^{b}	0.11 ± 0.07^{b}	0.08 ± 0.06	0.00 ± 0.00^{b}	0.97 ± 0.55^{aB}	0.000 ± 0.000^{bB}	0.87 ± 0.80
	Phytate	0.04 ± 0.02^{b}	0.72 ± 0.39^{b}	0.08 ± 0.03^{b}	0.06 ± 0.02	0.00 ± 0.00^{b}	7.57 ± 4.52^{aA}	0.005 ± 0.003^{bA}	0.82 ± 0.18^{b}
	Struvite	0.03 ± 0.00^{ab}	0.50 ± 0.13^{b}	0.07 ± 0.01^{ab}	0.05 ± 0.01	0.00 ± 0.00^{b}	1.35 ± 0.37^{bB}	0.004 ± 0.001^{aAB}	0.52 ± 0.18^{ab}
Mustard	$FePO_4$	0.02 ± 0.00^{b}	0.44 ± 0.07^{b}	0.00 ± 0.00^{d}	0.05 ± 0.01	0.00 ± 0.00^{b}	0.16 ± 0.02^{b}	0.000 ± 0.000^{b}	0.42 ± 0.04
	Phytate	0.02 ± 0.00^{b}	0.42 ± 0.10^{b}	0.00 ± 0.00^{c}	0.06 ± 0.01	0.00 ± 0.00^{b}	0.14 ± 0.01^{d}	0.000 ± 0.000^{c}	0.54 ± 0.19^{b}
	Struvite	0.04 ± 0.02^{b}	0.63 ± 0.38^{b}	0.04 ± 0.05^{b}	0.07 ± 0.03	0.00 ± 0.00^{b}	0.19 ± 0.06^{d}	0.000 ± 0.000^{b}	0.56 ± 0.15^{ab}

Numbers show means ± standard deviations. Different lowercase letters indicate significant differences ($p<0.05$) among the plant species, tested separately for each P source. Different capital letters indicate significant differences among the P sources, tested separately for each plant species. Absence of letters indicates that there was no significant difference

(Rech et al. 2019). We further found that soy exuded more LMWOA, mostly malonate, citrate, and malate, than the other plant species when supplied with struvite (Fig. 4; Table 2). Thus, soy might have mobilized P from struvite via a high LMWOA exudation, since in water only 1–2% of struvite P is soluble while in citric acid solution about 50–100% of struvite P is soluble (Ahmed et al. 2018; Cabeza et al. 2011; Möller et al. 2018; Rech et al. 2019). Moreover, dicarboxylic LMWOA (malate and oxalate) have been shown to mobilize slightly more P from struvite than citrate (Talboys et al. 2016). Further, the low LMWOA exudation of lupin found here (Fig. 4) might explain the comparatively low P content of lupin when P was provided in the form of struvite (Fig. 1).

We further found that the root length of soy tended to be larger than of the other plant species (Fig. S3; Supplement). This might have been advantageous for P uptake by soy once P was mobilized, since a strong positive linear correlation between root length and P uptake has been reported earlier (Pang et al. 2015). This is further supported by our finding that mustard had both the second highest plant P content (Fig. 1) and the second largest root length when supplied with struvite (Fig. S3; Supplement), while LMWOA exudation of mustard was low (Fig. 4). The advantage of a large root length for P mobilization from finely ground struvite has also been suggested for other *Brassicaceae* (Brennan and Bolland 2001; Lyu et al. 2016; Wen et al. 2021). By contrast, maize and lupin had comparatively low root lengths (Fig. S3; Supplement), which might be the reason for the lower P content of maize and lupin (Fig. 1). Our finding that mustard had the second highest plant P content when supplied with struvite (Fig. 1) is in accordance with studies on other *Brassicaceae* such as canola, in which P mobilization from struvite was high (Ahmed et al. 2018; Brennan and Bolland 2001; Katanda et al. 2016).

Mustard effectively mobilized P from $FePO_4$ likely through rhizosphere alkalinization

Our finding that mustard had the highest P concentration of all investigated plant species when supplied with $FePO_4$ (Table 1) indicates that mustard has a high potential to mobilize P from $FePO_4$. This is in accordance with a previous study reporting that the *Brassica* oilseed rape mobilized more P from $FePO_4$ than wheat and different legumes (Pearse et al. 2007). We further found that the pH in the exudate solution of mustard was higher than of the other plant species (Fig. 3). Thus, mustard might have mobilized P from $FePO_4$ via rhizosphere alkalinization since the solubility of $FePO_4$ increases with increasing pH (Hinsinger 2001; Lindsay 1979). Such pH increases in the rhizosphere have also been found for other *Brassicaceae*, which increased the rhizosphere pH by up to one pH unit compared to bulk soil (Marschner et al. 2007). Moreover, a significant positive correlation between the pH of rhizosphere extracts and leaf P concentrations has been reported for the *Brassica* oilseed rape when supplied with various P sources including $FePO_4$ (Pearse et al. 2007). We further found that the root length of mustard tended to be larger than of maize and lupin when supplied with $FePO_4$ (Fig. S3; Supplement), which might have been advantageous for P uptake by mustard, as discussed above. A significant positive correlation between shoot P uptake and total root length of different *Brassicaceae* and *Poaceae* supplied with $FePO_4$ has been reported earlier (Marschner et al. 2007; Wang et al. 2007a). The authors suggested that the large root length allowed the *Brassicaceae* to access a greater soil volume than wheat, resulting in root foraging for P in addition to P mining. However, it was also reported that P uptake and root length of the *Brassicaceae* correlated mainly in early growth stages (Marschner et al. 2007; Wang et al. 2007a).

The P concentration of lupin supplied with $FePO_4$ was significantly higher than of lupin supplied with phytate (Table 1). A higher capacity to mobilize P from $FePO_4$ than from phytate has also been reported for white lupin and chickpea (Shu et al. 2007; Wang et al. 2007b). However, since pH in the exudate solution of lupin was significantly lower than of mustard (Fig. 3) and LMWOA exudation of lupin was significantly lower than of soy and lower with $FePO_4$ than phytate (Fig. 4), the mechanisms of P mobilization from $FePO_4$ by lupin remained largely unclear. This indicates that LMWOA amount and composition as well as pH in the exudate solution alone do not explain lupins' ability to mobilize P from $FePO_4$, as has also been found in another experiment comparing different plant species and their utilization of different P sources (Pearse et al. 2007). However, lupin has been shown to effectively mobilize P from $FePO_4$ in

another experiment, likely through a high LMWOA exudation (Schwerdtner et al. 2022).

Legumes differed in their response to phytate

When P was provided in the form of phytate, plant P content of lupin was significantly lower than of soy (Fig. 1), while phosphomonoesterase activity was considerably higher in the rhizosphere of lupin than of soy (Fig. 3). One explanation for the contrasting findings among lupin and soy might be that soy exuded more phytases capable of catalyzing phytate hydrolysis, whereas lupin exuded mainly other phosphomonoesterases, not capable of hydrolyzing phytate. This is in accordance with former studies showing that the phytase activity of lupin (and other plant species) contributed less than 5% to total phosphatase activity (Gilbert et al. 1999; Hayes et al. 1999; Richardson et al. 2000), whereas soy has been shown to have a high phytase activity relative to other phosphatases (Ramesh et al. 2011). We further found that the maximum phosphomonoesterase activity per root surface, determined by soil zymography, was similar in the rhizosphere of lupin and soy (Figs. S2 and S4; Supplement), indicating that soy also had a few root regions with very high phosphomonoesterase activities. We cannot exclude that the phytase activity by soy was not (fully) detected by our analyses since (some) phytases might specifically catalyze the hydrolysis of phytate, but not of other phosphomonoesters (such as 4-methylumbelliferyl phosphate used in our analyses), thus potentially underestimating the total phosphomonoesterase activity of soy (German et al. 2011; Oh et al. 2004; Turner et al. 2002).

We further found that soy exuded significantly more DOC than the other plant species (Table 2). These organic substances (including LMWOA) might act as substrate for microorganisms, which produce additional phytases that effectively hydrolyze phytate in the rhizosphere of soy, as demonstrated earlier (Lambers et al. 2008; Wang and Lambers 2020; Wu et al. 2018). This is supported by previous studies showing that the addition of commercial fungal phytases (Hayes et al. 2000; Sun et al. 2021) as well as the inoculation with phytate-mineralizing bacteria (Ramesh et al. 2011; 2014; Richardson et al. 2000) increased P availability from phytate for soy, wheat, and several pasture species. Similarly, mycorrhizal symbionts have been found to effectively mobilize P from phytate (Wang et al. 2017; Zhang et al. 2016). Thus, in the case of soy (but not of non-mycorrhizal lupin), the so-called tripartite symbiosis, i.e., a double symbiosis with rhizobia and mycorrhizal fungi, might have contributed to phytate mineralization, as reported earlier (Bai et al. 2017; Jia et al. 2004).

Taken together, the P content of soy was highest among the investigated plant species in our study indicating effective P mobilization by soy. Soy mobilized P from phytate likely via high enzyme activity and high DOC exudation, and from struvite likely via high LMWOA exudation.

Implications

Overall, our study indicates that plant responses to different P sources were plant species-specific rather than P source-specific. The plant species-specific differences in P mobilization could be utilized to design multi-species plant communities that sustainably improve plant P nutrition in agriculture. For instance, the reliance on phosphate rock-derived fertilizers in agriculture could be reduced in intercropping systems with plant species that have complementary P mobilization capacities (Homulle et al. 2022; Honvault et al. 2021; Sulieman and Mühling 2021). The plant P content of maize was generally lower than of soy, mustard, and lupin (Fig. 1) and maize P concentrations (Table 1) indicate that maize P acquisition was relatively low (Reuter and Robinson 1997). Thus, maize plants could potentially benefit from intercropping with one of the other plant species if the different plant species have a joint rhizosphere in which complementary and facilitative interactions can occur. Such positive intercropping effects on maize have been proposed earlier in various studies on intercropping (Homulle et al. 2022; Li et al. 2020a; Schwerdtner and Spohn 2021; Tang et al. 2021). Moreover, plant species that effectively mobilize P from different soil P pools (such as soy and mustard) could potentially be used in crop rotations and/or as cover crops with likely positive effects on the P uptake of subsequent crops (Hallama et al. 2019).

Conclusion

In the present study, we found plant species-specific responses to different P sources. In particular, we found that soy had a high potential to mobilize P from struvite and phytate, while mustard had a high potential to mobilize P from $FePO_4$. Our findings suggest that soy effectively mobilized P from struvite via a high LMWOA exudation, which might be further promoted by its long roots. This partly confirms our first hypothesis on P mobilization via LMWOA from struvite, while it needs to be rejected for $FePO_4$. Our findings further suggest that mustard effectively mobilized P from $FePO_4$ via rhizosphere alkalinization, confirming our second hypothesis. We further found that soy but not lupin was capable of effectively mobilizing P from phytate, while phosphomonoesterase activity was considerably higher in the rhizosphere of lupin than of soy, indicating that the phosphomonoesterases that were determined here likely do not hydrolyze phytate. Our third hypothesis that a high phosphomonoesterase activity in the rhizosphere effectively mobilizes P from phytate needs, therefore, to be rejected.

Taken together, particularly soy and mustard were capable of mobilizing P from inorganic and organic sources through species-specific mechanisms. Thus, these plant species with their specific P mobilization mechanisms offer a chance to reduce the reliance of agricultural production on phosphate rock-derived fertilizers.

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Author contributions US and MS designed the study. US performed the greenhouse experiment. US and UL performed plant and exudate analyses. US wrote a first draft of the manuscript, US and MS worked on the manuscript. All authors read, contributed to, and approved the final version of the manuscript.

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Data availability The data generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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