

Role of Soil Minerals on Organic Phosphorus Availability and Phosphorus Uptake by Plants

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Abstract

Aims

Organic P (OP) accounts for significant fractions of the total phosphorus (P) pool in soils, especially in soils treated with organic inputs. In soils, OP compounds can be sorbed onto soil minerals but the consequences of these interactions on P availability and plant uptake are poorly known. This research aims at elucidating the extent to which adsorbed OP compounds to major soil minerals may be available to plants.

Methods

Ryegrass (*Lolium multiflorum*) plants were grown in RHIZOtest devices in the presence of OP (myo-inositol hexakisphosphate (IHP), glycerophosphate (GLY) and glucose-6-phosphate(G6P)) and inorganic P (IP) compounds that were previously adsorbed onto Fe and Al oxides (goethite and gibbsite, respectively) and clay minerals (montmorillonite and kaolinite). Phosphorus availability and P uptake were then determined through rhizosphere and plant characterization.

Results

Irrespective of the type of mineral, ryegrass was able to take up about 3-18% of adsorbed OP compounds. The magnitude of availability and uptake depended on the OP compounds and the type of soil minerals. The potential availability of OP adsorbed by different minerals was strongly mediated by mineral-OP interaction types and properties. The P uptake increased in the following order: kaolinite-OP << gibbsite-OP ≤ goethite OP << montmorillonite-OP. Phosphorus uptake from adsorbed OP compounds showed contrasting pattern compared to adsorbed IP and depended on available P in the rhizosphere and not necessarily on the binding strength of OPs to the mineral surface.

Conclusions

Unravelling the role of both OP and soil minerals properties on P availability constitutes an important knowledge to understand P dynamic in soil-plant system. Our results evidenced that the forms of OP adsorbed on Fe and Al oxides or clay minerals are available for plants to an extent which is strongly driven by OP forms and mineral types.

Introduction

Phosphorus (P) is a limiting nutrient in agroecosystems due to its strong sorption with soil particles which limits its availability for plants. The depletion of the world's phosphate rock reserves used to produce mineral fertilizers is now threatening food security (Filippelli, 2008; Reijnders, 2014). Recycling P from organic input becomes a necessity for sustainable P management in agroecosystems (Elser et Bennett 2011; Houben et al. 2017). However, P contained in organic input and soil occur under various inorganic and organic forms that differ in their availability to plants (Faucon et al., 2015; Kahiluoto et al.,

2015). The predominant OP forms in organic input include IHP, GLY and G6P (Giles et al., 2011; Vincent et al., 2013). Each compound differs from the others in its P content, type of P bond and size of the molecule (Amadou et al., 2021). These biochemical properties are likely to impact their availability to plants as they govern their interactions with the solid phases. Most research on the fate of P applied to soil has focused on IP compounds, showing that most of it is adsorbed at the surface of soil particles, which in turn influences its availability to plants (Hinsinger 2001; Houben et al. 2011). In contrast, the dynamics of OPs and their availability have been understudied to date, and knowledge about the contribution of these compounds to plant nutrition is still lacking (Faucon et al., 2015; Haygarth et al., 2018; Mezeli et al., 2019).

Soil minerals such as iron (Fe) and aluminium (Al) oxides (e.g. goethite and gibbsite, respectively) and clay minerals (e.g., kaolinite, montmorillonite) are major components of soils and sediments. They have received considerable attention due to their high P adsorption capacity (Bortoluzzi et al., 2015; Ryan et al., 2001) which may cause an OP utilization efficiency in soils as low as 5-10% (He et al., 1994). This leads to poor utilization of OP sources in agroecosystems (Amadou et al., 2021; Sulieman and Mühling, 2021). Indeed, OP compounds adsorbed on minerals were found to be the most stable P forms in different soil types (Martin et al., 2002; Montalvo et al., 2015). This has been attributed to their specific binding mechanism. Indeed, it was found that the number of the phosphate groups in a certain OP compound is determining the stability of its complex with the mineral surface (Anderson and Arlidge, 1962). For instance, IHP with its six phosphate groups generally exhibits a strong binding and high stability as compared with other OP or IP compounds which have a smaller number of phosphate groups. Ognalaga et al., (1994) showed that up to four phosphate groups of IHP interact with goethite surface, leading to formation of inner-sphere complexes between the IHP phosphate groups and the goethite surface. A similar mechanism has been suggested for other OP-mineral complexes. Desorption of P from mineral surfaces would be more limited for OP compounds compared to IP (Gerke, 2015; Ruttenberg and Sulak, 2011). However, the extent to which OPs adsorbed to soil minerals can desorb remains poorly known and their availability to plants is still debated.

Several authors have suggested that the mineral-OP bridging compounds are not available to plants because these complexes are formed during the slow reaction phase with soil minerals (Hingston et Quirk 1974; Barrow et Shaw 1975). This process has been hypothesized to be a major cause of plant growth limitation (Javaid, 2009). After several desorption cycles, Martin et al., (2002) found that 20% of IP desorbed from goethite while it only accounted for less than 5% for IHP. Similar findings were reported by Ruyter-Hooley et al., (2015) with limited desorption of IHP (<3% of total amount) on gibbsite, even in the presence of humic acids as competing ligands for sorption sites. In addition, Gerke, (2015) proposed that the presence of Ca in soil solution might further reduce IHP solubility and availability due to the formation of Ca-IHP precipitates. These studies suggest that the availability of OP is probably mainly limited by its solubility and not by enzymatic activity (Gerke, 2015; Lung and Lim, 2006). This is corroborated by plant growth tests in the presence of synthetic goethite (Martin et al., 2002) and in P-fixing soils (Adams and Pate, 1992) where sorption and/or precipitation also lowered the IHP solubility and subsequent bioavailability. In any case, there was a greater affinity of the OP compounds for soil minerals than that

of the IP compounds, indicating the formation of a very stable complex of OPs with mineral surfaces. Thus, it can be expected that desorption and plant availability of mineral-OP complexes are more difficult than those of IP compounds, although this has never been quantitatively defined. There is also some experimental evidence that most of the P taken up by plants originates from the soil mineral-OP complex, although adsorbed OP is not easily or widely desorbed (Ahmed et al., 2021; He et al., 1994). This implies that OP associated with soil minerals is potentially available to plants, although its availability also depends on the type of soil minerals and the OP compound (Andrino et al., 2019; D'Amico et al., 2020). Recently, D'Amico et al. (2020) exposed mesh bags filled with goethite associated with IP or IHP for 13 months to P-deficient soils in the Italian Alps. More P (45% of IHP vs 65% of IP) was lost from the mesh bags, indicating a direct release of both OP and IP from the mineral surfaces. The extent of OP release was smaller than that of IP release. In general, the majority of studies that aim to better understand P availability in soils are based on the IP form. The very few studies on OP do not adequately quantify their potential contribution to P availability in the organic fertilizer-soil-plant system (Amadou et al., 2021; Klotzbücher et al., 2020; Sulieman and Mühlhling, 2021). For example, although some studies consider IHP as a source of available P, its availability in the presence of the major soil minerals remains poorly understood (Garcia-Lopez et al., 2015; Martin et al., 2002). Moreover, these studies did not consider other important P pools such as GLY or G6P which, together with IHP, nevertheless represent an important part of the total P in the soil (Darch et al., 2014; Gérard, 2016). Furthermore, the soil minerals used were in most cases goethite; the involvement of Al oxides and clays being neglected (Gérard, 2016). To our knowledge, there are no studies that evaluate and compare the availability of P to plants from the major OP compounds (IHP, GLY, and G6P) that were adsorbed onto the major soil minerals (Fe and Al oxides and clay minerals). It is therefore crucial to understand the complex mechanisms that control the dynamics of important compounds of OP in major soils fertilized with organic inputs and the efficiency of the OP-minerals interaction in supplying P to crops.

This study was set up in order to identify the extent to which OP bound to Fe and Al oxides and clay minerals complexes contributes to plant P acquisition. This could open up possibilities for the use of renewable nutrient-rich organic amendments according to different soil mineral properties. Specifically, we determined the plant P availability from several complexes of IHP, G6P, and GLY that were adsorbed onto synthetic Fe and Al oxyhydroxides (goethite and gibbsite) and clay minerals (kaolinite and montmorillonite). Mineral-IP complexes with KH_2PO_4 were also carried out for comparison. The P uptake for each compound was determined using ryegrass grown in RHIZOtest device. The two main following hypotheses were addressed: (1) P from adsorbed OP compounds is available to ryegrass and varies with soil mineral properties; (2) the relative P uptake of the different complexes OP-minerals are dependent with their binding strength and (3) adsorbed OP compounds on all minerals tested are less available than adsorbed IP because it desorbs less and requires not only desorption but also enzymatic cleavage before being taken up by ryegrass.

Materials And Methods

Organic P compounds and individual soil minerals

Organic P compounds, IHP, GLY, G6P and one IP (KH_2PO_4) were selected for experiments. Such OP compounds were initially selected based on their predominance in organic inputs and soils, the types of P bonds and their different molecular sizes. The soil minerals were selected to be representative of the predominant minerals in soils. Four individual soil minerals were used. Goethite [$\text{Fe}(\text{OH})\text{O}$] and gibbsite [$\text{Al}(\text{OH})_3$] were chosen as representative of Fe and Al oxides; kaolinite and montmorillonite were selected as clay minerals, particularly 1:1 phyllosilicate and 2:1 phyllosilicate respectively. All minerals were obtained from Sigma-Aldrich Chemie S.a.r.l. and VWR (France) for experimentation.

Preparation of minerals-P Adsorption Complexes

The four soil minerals were loaded with the tree OP compounds or inorganic P to serve as P source for ryegrass. Solutions containing 1 g P L^{-1} in 0.1 M KCl at pH 5.5 were prepared using the different P compounds. Goethite, gibbsite, kaolinite and montmorillonite was weighed in portions of 100 g into 1-L bottles. Then, 200 mL of 0.1 M KCl were added and the bottles were shaken for 24 hours at 25°C to sufficiently hydrate the adsorption sites on the minerals. The pH was maintained at 5.5 ± 0.05 by adding 0.1 M HCl or NaOH solution. To start the formation of OP-mineral complexes, each of the 1 L bottles containing the soil minerals was filled with 800 mL of each P solutions. In each bottle containing both the soil minerals and P compounds, some drops of hexanol were added to suppress microbial activities. Bottles were shaken on a mechanical shaker for 24 hours at 25°C and then centrifuged (3000 g for 15 minutes). The 1 L bottles were distributed into several 250-mL bottles, centrifuged, and the supernatants were collected and removed. The produced P-loaded minerals were agitated in deionized water and frozen at -20°C . To determine the amounts of adsorbed P, a certain volume of supernatants was immediately filtered through a $0.22\text{-}\mu\text{m}$ membrane syringe filter for P analysis. The concentration of P in the supernatants was determined calorimetrically (Ohno and Zibilske, 1991) after hydrolyzing OP to IP using the persulfate oxidation method (Peters and Van Slyke, 1932). The quantity of P adsorbed was calculated as the difference between the initial amount of P added and the remaining P amount in supernatant at the end of the experiment. The P loadings of the mineral-P complexes produced are shown in Table 1. All minerals were loaded to reach their adsorption maxima.

Table 1 P adsorption capacity of the produced minerals-P adsorption complexes

Soil minerals	P compounds	Quantity of P adsorbed ($\mu\text{g g}^{-1}$)
Goethite	IP	2810
	IHP	3742
	GLY	1398
	G6P	4337
Gibbsite	IP	20949
	IHP	56698
	GLY	6237
	G6P	5588
Kaolinite	IP	1736
	IHP	6082
	GLY	1222
	G6P	2295
Montmorillonite	IP	3709
	IHP	4857
	GLY	1045
	G6P	2338

Characterization of OP desorption

A KCl extraction was carried out to characterize the strength or energy with which P forms are bound to soil minerals. Extractions were carried out by adding 40 mL of 0.1 M KCl adjusted to pH 5 to 0.5g minerals-P complex. Samples were shaken on a mechanical shaker at 25°C during 24h. After centrifugation for 10 minutes, 5 mL of the supernatant was taken for the measurement of P concentration by the same molybdenum blue method. This solution P concentration was defined as the desorbed P.

Experimental Setup and Plant growth

We used the RHIZOtest device (MetRHIZlab, France) designed by Bravin et al., (2010) which consists in separating plant roots from soil with a 30-mm polyamide mesh to facilitate the collection of roots and rhizosphere (Houben and Sonnet, 2015). As described by Gómez-Suárez et al. (2020), in a first step (preculture period), 0.20 g of ryegrass (*Lolium multiflorum*) seeds were grown for 14 days in hydroponics in a cylinder closed at the bottom with a 30 μm polyamide mesh allowing the development of a dense, planar root mat with nutrient solution: $\text{Ca}(\text{NO}_3)_2$ (2 mmol L^{-1}), MgSO_4 (0.5 mmol L^{-1}), K_2SO_4 (0.7 mmol L^{-1}), KCl (0.1 mmol L^{-1}), KH_2PO_4 (0.1 mmol L^{-1}), MnSO_4 (0.5 $\mu\text{mol L}^{-1}$), CuSO_4 (0.5 $\mu\text{mol L}^{-1}$), ZnSO_4

($0.5 \mu\text{mol L}^{-1}$), $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$ ($0.01 \mu\text{mol L}^{-1}$) and Fe-EDTA ($100 \mu\text{mol L}^{-1}$). In a second phase (cultivation period), the two-week-old seedlings, showing a dense root mat, were transferred to a thin layer of soil made of different mineral-P complexes previously prepared and acid washed quartz. The amount of mineral-P complex added in the mixture was calculated to supply 40 mg of P while the amount of quartz was calculated to reach a final mass of 10 g, which corresponded to a 1.5-mm thick soil layer. The soil layer was then connected to 500 mL nutrient solution with a filter paper wick. The composition of this nutrient solution was the same as that used for the preculture period except that P was not added. In order to provide the same amount of P in each treatment, 40 mg of P was added with an adequate mass of each mineral-P complex. The RHIZOtest devices were placed in controlled conditions (phytotron) under a photoperiod of 12h, constant temperature ($25 \text{ }^\circ\text{C}$) and relative humidity (80%). Unplanted control treatments, in which the quartz - mineral-P complex had been incubated in similar devices without plants (thereafter called bulk soil), were also conducted. In total, 128 such devices were implemented: 4 P compounds (IHP, GLY, G6P and IP) x 4 soils minerals (goethite, gibbsite, kaolinite and montmorillonite) x 2 crop conditions (ryegrass and bulk soil) x 4 replicates.

Plant sampling and analysis

The plants were harvested after 15 days of contact with mineral-OP complexes. At harvest, shoots and roots were separated and roots were gently rinsed with deionized water. Shoots and roots were then dried at $60 \text{ }^\circ\text{C}$ for 72 h, weighed and crushed prior to analysis. The concentration of P in shoots and roots was determined calorimetrically (Ohno and Zibilske, 1991) after mineralization by 65% HNO_3 digestion directly in a microwave Teflon vessel (Lange et al., 2014). Total plant P uptake was calculated by summing P uptake by roots (i.e., root P concentration multiplied by root dry mass) and P uptake by shoot (i.e., shoot P concentration multiplied by shoot dry mass).

Rhizosphere and bulk soil analyses The availability of P in the rhizosphere and the bulk soil collected at the end of the RHIZOtest experiment was assessed by anion exchange membrane (Nobile et al., 2019). Masses equivalent to 0.5 g (mineral-P + quartz) of the collected mineral-P complexes were added to 50 mL bottles with 30 mL deionized water and two strips of anion exchange membrane. The whole set was mixed and stirred for 16 h. The membranes were then removed and rinsed in deionized water and the P recovered by shaking for 1 h in 20 mL of 0.5M HCl. Phosphorus concentrations were analyzed by calorimetry using a spectrophotometer (610 nm).

Data processing and analysis

Data were statistically analyzed with R software. The impact of factors (P compounds, soil minerals and their combined effect) on P availability and uptake was modeled by generalized linear models (GLM) using the "FactomineR" package. All factors were tested individually and the models were compared on the basis of second-order Aikake information (AICc), with the lowest relative value being considered the best fit. The anova of the best-fit GLM model with a chi-square test generates the deviance analysis table that gives the significance level of all factors.

Results

Biomass Production

Total biomass varied slightly between treatments (Table2). Although there was a significant difference between goethite and gibbsite for IHP forms, total biomass did not vary significantly between treatments. Some weak differences could be observed between soil mineral types. The lowest biomass was observed with the Gib-Po complex and the highest with the K-Po complex. In general, except on gibbsite, the mineral-Po complexes produced equal or slightly more total biomass than the mineral-IP complexes.

Table 2 Biomass of root, shoot and the whole plant (root + shoot biomasses). Different letters indicate significant differences between treatments ($p < 0.05$)

	Root Biomass (g)	Shoot Biomass (g)	Total Biomass (g)
Go-IP	0.27	0.55	0.82 ± 0.10 ab
Go-IHP	0.27	0.85	1.12 ± 0.13 a
Go-GLY	0.33	0.64	0.96 ± 0.12 b
Go-G6P	0.27	0.54	0.81 ± 0.19 ab
Gib-IP	0.26	0.60	0.86 ± 0.16 a
Gib-IHP	0.17	0.42	0.60 ± 0.25 bc
Gib-GLY	0.19	0.43	0.62 ± 0.12 ab
Gib-G6P	0.21	0.45	0.66 ± 0.07 ab
K-IP	0.22	0.83	1.05 ± 0.15 ab
K-IHP	0.18	0.61	0.79 ± 0.16 bc
K-GLY	0.28	0.85	1.13 ± 0.20 a
K-G6P	0.27	0.75	1.02 ± 0.13 ab
M-IP	0.21	0.72	0.93 ± 0.12 a
M-IHP	0.19	0.68	0.87 ± 0.20 a
M-GLY	0.23	0.72	0.95 ± 0.22 a
M-G6P	0.27	0.71	0.98 ± 0.19 a

Combined effects of organic P and soil minerals on P uptake

The impact of P compounds, soil minerals, and their combined effect on total P uptake by ryegrass was modeled by GLM (Table 3). Variations in P uptake by ryegrass were significantly affected by P compounds and their interaction with soil minerals. As shown by the lower AIC values (Table 3), the variation was more dependent on the interaction between minerals and P compounds. During the

growing season, P recovered by ryegrass was 21%-28% from adsorbed IP, 0%-5% from adsorbed IHP, 4%-18% from adsorbed GLY, and 2%-9% from adsorbed G6P, depending on the mineral type (Fig 2).

Table 3 The GLM model results testing impact of factors (P compounds, soil minerals and their combined effect) on total P uptake

Variables effects	P uptake	
	<i>p-value</i>	<i>AIC</i>
P forms	<0.001	268-329
Minerals: P forms	<0.001	156-199
Soil minerals	<0.001	314-388
R ²	0.92	

Effect of OP compounds on P uptake by ryegrass

With the exception of kaolinite, P uptake by ryegrass varied significantly between the adsorbed OP compounds (Table 4). Differences in total P uptake between OP compounds decreased in the order GLY >> G6P > IHP (Fig 2). Phosphorus concentrations in roots and shoots were higher under the adsorbed GLY compound than under the other OP compounds (Fig 2). Of all OP compounds, adsorbed IHP was the lowest supplier of P to ryegrass. Compared to IP, P uptake from adsorbed OP compounds was highly contrasted and dependent on the specific compounds of OP. Phosphorus uptake from adsorbed IHP and G6P was significantly lower than that from adsorbed IP, with the order being: IP >> G6P > IHP (Fig 2). However, the trend was different for the adsorbed GLY compound, which, depending on the minerals, was in this order IP = GLY (goethite and montmorillonite) or in this order GLY >> IP (gibbsite). Thus, P uptake from GLY adsorbed on goethite and montmorillonite was similar to the adsorbed IP compound while P uptake from GLY adsorbed on gibbsite was significantly higher than IP. In sum, OP adsorbed on soil minerals was available to ryegrass since the plant was able to take up a certain amount of it even if it was relatively low from certain mineral-OP complexes, e.g., mineral-IHP complexes. Moreover, P uptake was highly variable and strongly dependent on the characteristics of the OP compounds.

Table 4 One-way ANOVA results testing the effects of OP compounds by soil minerals on total P uptake, P availability and dry weight

Variables effects	P uptake	Dry weight
	<i>p-value</i>	<i>p-value</i>
Go-OP	< 0.001	0.07
Gib-OP	< 0.001	0.92
K-OP	0.05	0.08
M-OP	<0.001	0.72

Relationships between P uptake, soil minerals-OP interaction and P availability

The P uptake was influenced by the soil mineral-OP interactions. Phosphorus uptake from OP adsorbed onto the four tested minerals increased in the following order: kaolinite-OP << gibbsite-OP ≤ goethite OP << montmorillonite-OP. A large difference was observed between kaolinite, Fe and Al oxides and montmorillonite in their ability to release P for plant uptake (Table 3 and Fig 2). The amount of P taken up from montmorillonite-OP complexes was the highest. On the other hand, P uptake from kaolinite-OP and gibbsite-OP (especially gib-IHP or G6P) was low. Overall, less than 4% of the initial adsorbed P was desorbed and mineralized for plant uptake.

Phosphorus uptake by ryegrass from mineral complexes was positively correlated with ΔP resin ($R = 0.73$, $p < 0.01$) (Fig 3). However, no correlation was found between P uptake, resin-extracted P concentration in the rhizosphere (Resin P), and P concentration extracted with KCl. In addition, the ΔP resin values of the majority of the mineral-OP were generally negative (Fig 4) even though some complexes, e.g., GLY-mineral complexes, showed almost nil ΔP resin values, i.e., no variation between resin P concentration in bulk soil and resin P concentration in the rhizosphere (Fig 4).

Discussion

Phosphorus from adsorbed OP compounds is available to plants

Our first hypothesis that P from adsorbed OP compounds is available to ryegrass and varies with soil mineral properties was confirmed in our experiment. The two main findings supporting the hypothesis are: the ryegrass was able to take up about 3-18% of OP adsorbed to soil minerals; OP compounds as well as their interactions with soil minerals significantly affected P uptake for ryegrass.

The amount of P recovered by ryegrass reached 5% from adsorbed IHP, 9% from G6P and 18% from adsorbed GLY. In general, P uptake decreased in the order GLY >> G6P > IHP. Taken together, these results indicate that, irrespective of soil mineral, adsorbed OP was at least partially available to plants. The magnitude of this availability depended on the OP compounds and the types of soil minerals. The extent to which adsorbed OP may be available for plant uptake remains poorly understood and controversial. Several authors have suggested that they are not available to plants (Barrow and Shaw, 1975; Guzman et al., 1994; Hingston et al., 1974), while others show experimental evidence of their availability and uptake by plants (Andrino et al., 2019; D'Amico et al., 2020; Parfitt, 1979). However, in all of these studies, the compound of P used was IP with only one compound of OP without considering other important OP pools such as GLY or G6P. Furthermore, the soil minerals used in most cases were Fe oxides, namely goethite, while Al oxides and clays have been ignored. To our knowledge, no study has evaluated and compared the availability of P to plants from the major OP compounds (IHP, GLY, and G6P) that were adsorbed onto the major soil minerals (Fe and Al oxides and clay minerals). Thus, our work after comparing several main soil mineral-OP complexes, argued that some amount of P can be available from the adsorbed OP compounds. Therefore, adsorbed OPs can act as a source of P in the soil depending on their availability of adsorbed species.

The availability of P from adsorbed OP differed between OP compounds. The P uptake from the adsorbed GLY compound was much higher than that of adsorbed G6P which was more available than adsorbed IHP. It appears that the difference in availability among the adsorbed phosphates was determined by the adsorption capacity more than their binding strength. The trend in availability (GLY >> G6P > IHP) would be mainly explained by the distinct sorption and desorption dynamics of the different minerals, leading to the lowest desorption for IHP-P, followed by G6P-P and then GLY-P. Basically, we expected G6P to be more available than GLY due to its higher desorption and mineralization rate and its likely instability on soil minerals due to its higher molecular weight than GLY (Annaheim et al., 2010; Annaheim et al., 2013; Ruttenberg and Sulak, 2011; Yan et al., 2014). The opposite result we found may be the consequence of its more negatively charged surface than GLY (Giaveno et al., 2008; Ruttenberg and Sulak, 2011). These reasons would also explain why the binding energy of G6P predicted from the Langmuir model is often higher than that of GLY or IP(Goebel et al., 2017). On the other hand, it may also mean that G6P was more desorbed than GLY but after desorption, its mineralization would have been lower, resulting in its low absorption by plants. Finally, adsorbed GLY was the higher source of P for plant uptake compared to other compounds, consistently with Adams and Pate (1992). In conclusion, the availability of OPs for plant nutrition from organic inputs and soil would be determined by the stability of OP-mineral complexes or by their (de)sorption dynamics. Consequently, the IHP would have formed with the minerals, stable complexes with multiple rings and had a lower availability than other OP compounds.

To summarize, the different OP compounds showed different availability to ryegrass. Phosphorus uptake decreased in the order GLY >> G6P > IHP. This trend is mainly explained by the (de)sorption capacities and strength of the different minerals, leading to the least desorption for IHP-P, followed by G6P-P and then GLY. The high uptake of P from adsorbed GLY is thought to be due to its low binding to soil minerals, high desorption and ability to be hydrolyzed by most soil enzymes. In addition difference in P uptake between adsorbed GLY, G6P, and IHP might also be related to their different degrees of hydrolysis by enzymatic activity as shown by Annaheim et al., (2010) and Bünemann, (2008). Hydrolysis of OP by enzymatic activity is generally affected by the chemical nature of P and especially its solubilization from soil minerals (Amadou et al., 2021; Greiner et al., 2007; He et al., 2004; He and Honeycutt, 2001; Richardson et al., 2005). Thus, higher molecular weight and higher phosphorylated compounds such as IHP may be more resistant to enzymatic activity especially when adsorbed, limiting their degradation from mineral surfaces. Thus, in addition to the nature of the OP compounds and their (de)sorption mechanisms, their capacity for hydrolysis by enzymes is also an important factor affecting their uptake by the plant.

Effect of mineral-OP interactions on P uptake by ryegrass.

The potential availability of phosphate adsorbed by different minerals was strongly affected by mineral-OP interactions properties. The P uptake increased in the following order: kaolinite-OP << gibbsite-OP ≤ goethite OP << montmorillonite-OP. Montmorillonite-OP complexes showed the highest P uptake, with a maximum of 18%. On the other hand, P uptake from kaolinite-OP was the lowest. Less than 4% of the

initially adsorbed P was desorbed and mineralized for plant uptake. These results indicated that regardless of the type of mineral and its sorption strength and stability toward OP, plants are able to take up at least a small portion of it for their nutrition. This agrees with laboratory and greenhouse studies indicating that specifically adsorbed P was potentially available to plants although it was very difficult to desorb (Bollyn et al., 2017; D'Amico et al., 2020; He et al., 1994; Martin et al., 2002; Montalvo et al., 2015; Parfitt, 1979; Shang et al., 1996). Thus, even under conditions where the activities of plant microbiomes and roots that can help mobilize P are limited, OP-mineral complexes still have potential for supplying P to plants.

Montmorillonite-OP complexes, in particular, montmorillonite-GLY or G6P were found to serve as sources of P in soils more than the other complexes. Organic P adsorbed on kaolinite was released the lowest amount of P to the plants. Overall, there was a considerable difference in P uptake between the tested minerals. Montmorillonite-OP complexes would provide more P due to the negative charges of montmorillonite i.e. its zero point of charge values (He et al., 1994) causing its weak binding to OP, resulting in the formation of unstable OP-montmorillonite complexes (He and Zhu, 1998; He et al., 1994; Hingston et al., 1974). The low P uptake from kaolinite-OP agrees with previous observations showing that kaolinite-P is an inner-sphere surface and bidentate complex below pH 6 (Hu et al., 2020; Ruyter-Hooley et al., 2015), and the adsorbed P on kaolinite is difficult to desorb (Kafkafi et al., 1988; Manning and Goldberg, 1996). Hence, our result emphasized that Fe and Al oxides were less responsible for limiting OP availability than kaolinite despite their general higher adsorption capacity in soil. Therefore, apart from the nature of the OP compounds, the characteristics of the minerals is an important factor responsible for the difference in P uptake between the tested OP-mineral complexes.

In sum, our results evidence that the type of minerals is a key driver of P availability for plant. Based on our results, all OP-mineral complexes can act as a sink or source of P in soil. Our results showed good utilization efficiency of all OP compounds adsorbed on montmorillonite, in particular, montmorillonite-GLY or G6P compared to other minerals. The kaolinite-OP complex released very low amounts of P, probably due to its high stability with OPs. The contrasted physicochemical properties (specific surface areas, net surface charges, interaction properties) of the minerals are likely the major mechanisms responsible for the chemical release of specifically adsorbed OP in the tested soils. Thus, efficiency of OP utilization by plants in agricultural soils following the addition of organic input will depend on the dominant soil type and its characteristics. Soils rich in 2:1 phyllosilicate would have a higher availability of OPs than soils rich in Fe and Al oxides, which in turn would have a higher availability of OPs than soils rich in 1:1 phyllosilicate. Obviously, more research is needed to understand and test this phenomenon under real field conditions.

No correlation was found between P uptake and resin-extracted P concentration (Fig 3). In addition, rhizosphere resin P concentration for most mineral-OP complexes was higher than that of the bulk soil. Hence, these results suggest that plants would have taken up additional pools of P beyond what was initially available, so the plant must have induced additional desorption of OP. According to Le Chatelier's principle (Law of Mass Action), the sink effect of roots caused an OP depletion in the solution, which in

turn induced further OP desorption dissolution to replenish the solution (Houben and Sonnet, 2012). In addition, mobilization of OP by ryegrass roots might also have contributed to OP depletion. As shown by Martin et al., (2002), high efficiency of ryegrass in displacing strongly bounded P may be due to the fact that the plant can react to P deficiency by extending root surface and utilizing more than one mechanism of extraction at the same time.

It is generally accepted that P extraction with KCl is negatively correlated with the binding energy of the P compounds to soils. Thus, the more P can be extracted with KCl to become available to plants, the lower its binding energy (Martin et al., 2004; Yan et al., 2014). However, our results showed no correlation between P uptake and P extracted with KCl. The lack of correlation in our case may imply that the P taken up by plants did not depend on the strength or energy with which OP compounds are bounded to soil minerals. Nevertheless, this lack of correlation between P taken up by plants and P extracted by KCl could also mean that OP compounds may have been released from the soil minerals but remained in organic form without being mineralized for uptake by plants. Therefore, we hypothesize that although OP was desorbed from some minerals, it may not have been absorbed because it was not readily hydrolyzable by enzymes. This supports our earlier explanation of the resistance of some of OP compounds to enzymatic hydrolysis because of their chemical properties.

Finally, P uptake by ryegrass was positively correlated with ΔP resin ($R = 0.73$, $p < 0.01$), showing that the variation of available P in the rhizosphere determined the P uptake by plant (Fig 3). The ΔP resin values of the majority of the mineral-OP complexes was generally negative, showing that in addition to the spontaneously released P, there would have been a subsequent release of P from soil minerals that would occur in response to plant-induced depletion of available P in the rhizosphere. This that plant roots mobilized additional P from minerals. However, this finding did not apply to all OP-minerals complexes. For instance, GLY-mineral complexes (Fig 4) showed almost no variation in ΔP resin, i.e. no variation between P resin in the bulk soil and P resin in the rhizosphere, suggesting that plant absorbed only the spontaneously available P without any other mobilization. This confirms that GLY was sufficiently available from soil minerals. Thus, when the plant was in the presence of soil minerals involving GLY, there was little or no additional P mobilization.

Here, we showed that the binding strength of OPs to the mineral surface did not necessarily explain P availability and uptake by plant. Furthermore, plant uptake, by inducing depletion of the available P pool, would have resulted in additional mobilization of OP. However, for some complexes, no additional mobilization was required due to sufficient P availability. Thus, plant P uptake from OP-mineral complexes may depend on the variation of available P in the rhizosphere, which results from (de)sorption dynamics and the ability of the plant species to mobilize specific OP compounds via its uptake effect or via physiological processes.

Phosphorus uptake from adsorbed OP relative to adsorbed IP

Our third hypothesis was that P from adsorbed OP would be less available than P from adsorbed IP because it desorbs less and requires also enzymatic cleavage before being taken up by ryegrass. Our

results support only partially this hypothesis as they showed that the different adsorbed OP compounds had contrasted P uptake compared to the adsorbed IP compound. Phosphorus uptake from adsorbed IHP and G6P was significantly lower than that of adsorbed IP, whereas P uptake from adsorbed GLY, depending on the mineral, was slightly equal or higher than that of IP. Several studies have shown lower plant availability of adsorbed OP compounds compared to IP compounds (Andrino et al., 2019; D'Amico et al., 2020; Klotzbücher et al., 2019), probably due to the specific binding mechanisms of OP and its low desorption from soil (Bollyn et al., 2017; Ruyter-Hooley et al., 2015). However, in all of these studies, "organic P" refers only to IHP. In addition to IHP, GLY and G6P are also commonly found in soils, soils treated with organic inputs, sediments, and wetlands (Missong et al., 2016; Vincent et al., 2013) but these OP forms have not been considered potential sources of P for plants, except in a few studies (Adams and Pate, 1992). Here, our results highlight the relative availability of these major OP forms compared to that of IP. In agreement with previous studies (Andrino et al., 2019; D'Amico et al., 2020; Ruttenberg and Sulak, 2011), IHP was less available than IP. Similar to IHP, we also found that adsorbed G6P was less available than IP. This might be explained by the greater adsorption and binding strength of G6P to external surface sites than IP (Goebel et al., 2017; Ruttenberg and Sulak, 2011). Finally, we found that the adsorbed GLY compound, depending on the minerals, was almost equivalent or more available than the IP compound. This is attributed to its low affinity for soil minerals and especially to its high desorption in soil. Thus, it can be inferred that soil amendment with organic inputs with high concentration of GLY might be a sustainable alternative to mineral P fertilizer.

In the present studies, GLY regardless of soil type was generally as available as IP. More importantly, we showed that on Al oxides, GLY was significantly more available than IP. Thus, based on comparisons of different P compounds, our results showed that in soil, unlike IHP, another major compound of OP such as GLY can be equal or superior to IP in terms of plant availability.

Conclusion

Our results demonstrate that adsorbed OP compounds may be a source of P for plants regardless of the type of mineral and its sorption capacity. The differences in P uptake between OP compounds were strongly mediated by soil mineral type, interaction properties i.e. (de)sorption mechanisms and their different degrees of hydrolysis by enzymatic activity resulting in P uptake decreasing in the order GLY >> G6P > IHP. Higher use efficiency of OP adsorbed on montmorillonite than on other minerals indicates that soils rich in 2:1 phyllosilicate might have greater P availability than soils rich in Fe and Al oxides or 1:1 minerals when they are amended with organic inputs. In addition, despite the lower P uptake from Al oxides compared to montmorillonite, we nevertheless observed a significant higher availability of GLY relative to IP. Thus, GLY would be less affected by minerals that limits P availability, which are especially found in the highly weathered soils of tropical regions. The binding strength of OPs to the mineral surface does not necessarily affect P availability to plants and the effect of plant uptake may result in additional P mobilization. Finally, the wide range of P uptake and availability in the presence of different mineral-OP complexes emphasized the importance of considering the chemical nature of OP and its ability to interact with soil minerals when attempting to improve soil OP cycling for plant use. As a further step, the role of

OP-soil minerals interactions on P availability should be unraveled according to the main P acquisition strategies (e.g. mining, foraging and intermediates strategies) to design sustainable P fertilization.

Declarations

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Figures

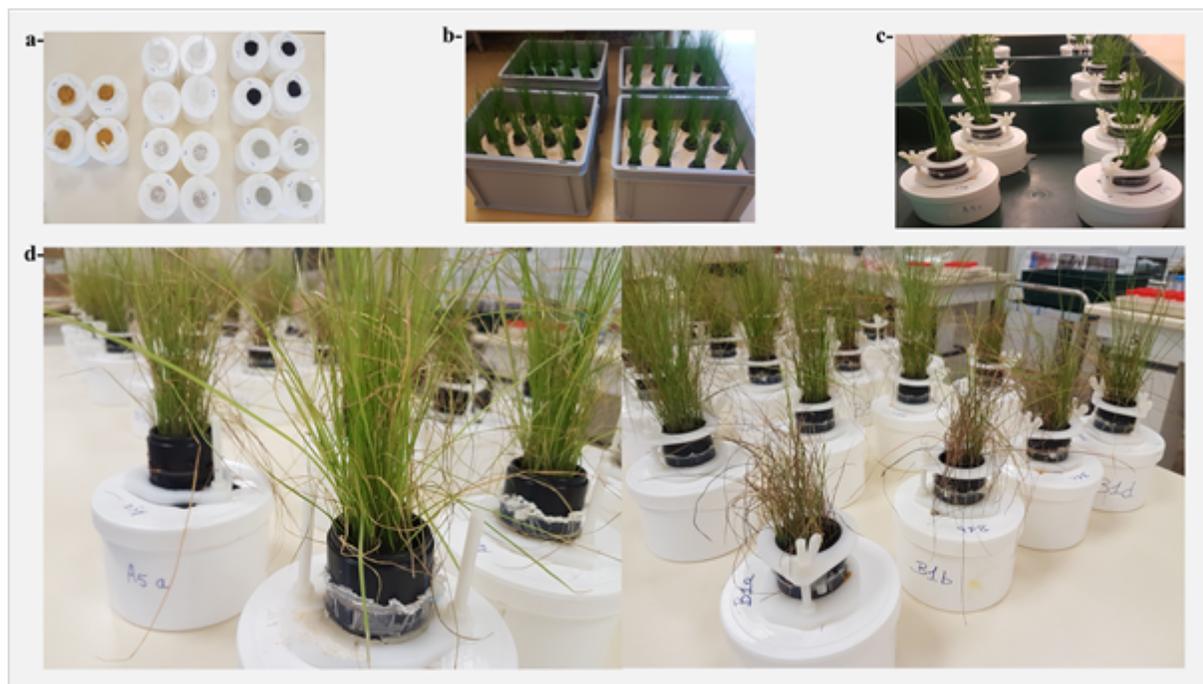


Figure 1

Picture of the experimental Setup and Plant growth using the RHIZOtest device: a- soil layer of quartz - mineral-OP complex; b- preculture period; c- contact between the soil and plant device; d- result at the end of the experiment

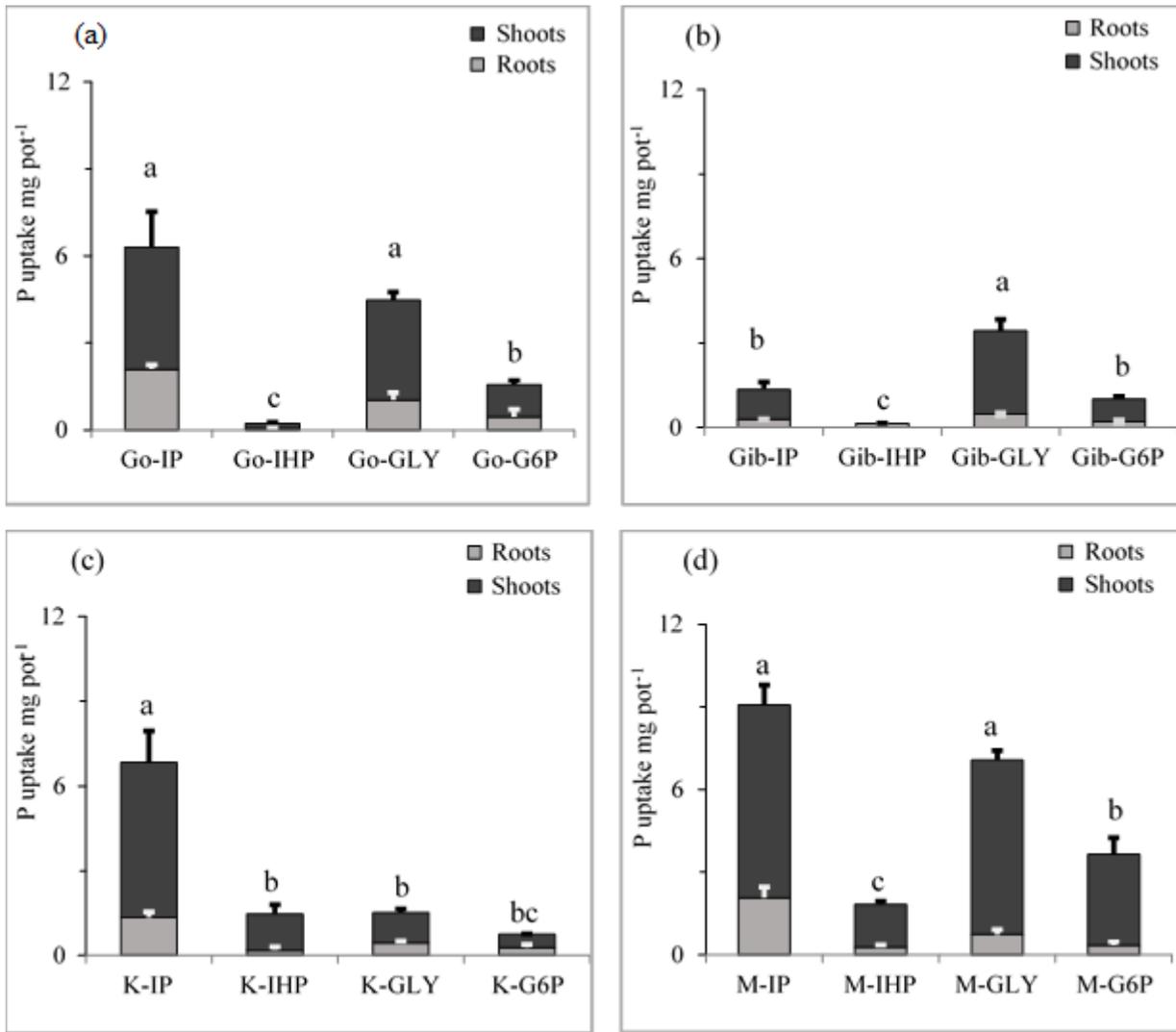


Figure 2

Phosphorus uptake by root and shoot ryegrass plants with different P sources. Different letters indicate significant differences between treatments for the total P uptake ($p < 0.05$). Error bars indicate standard error

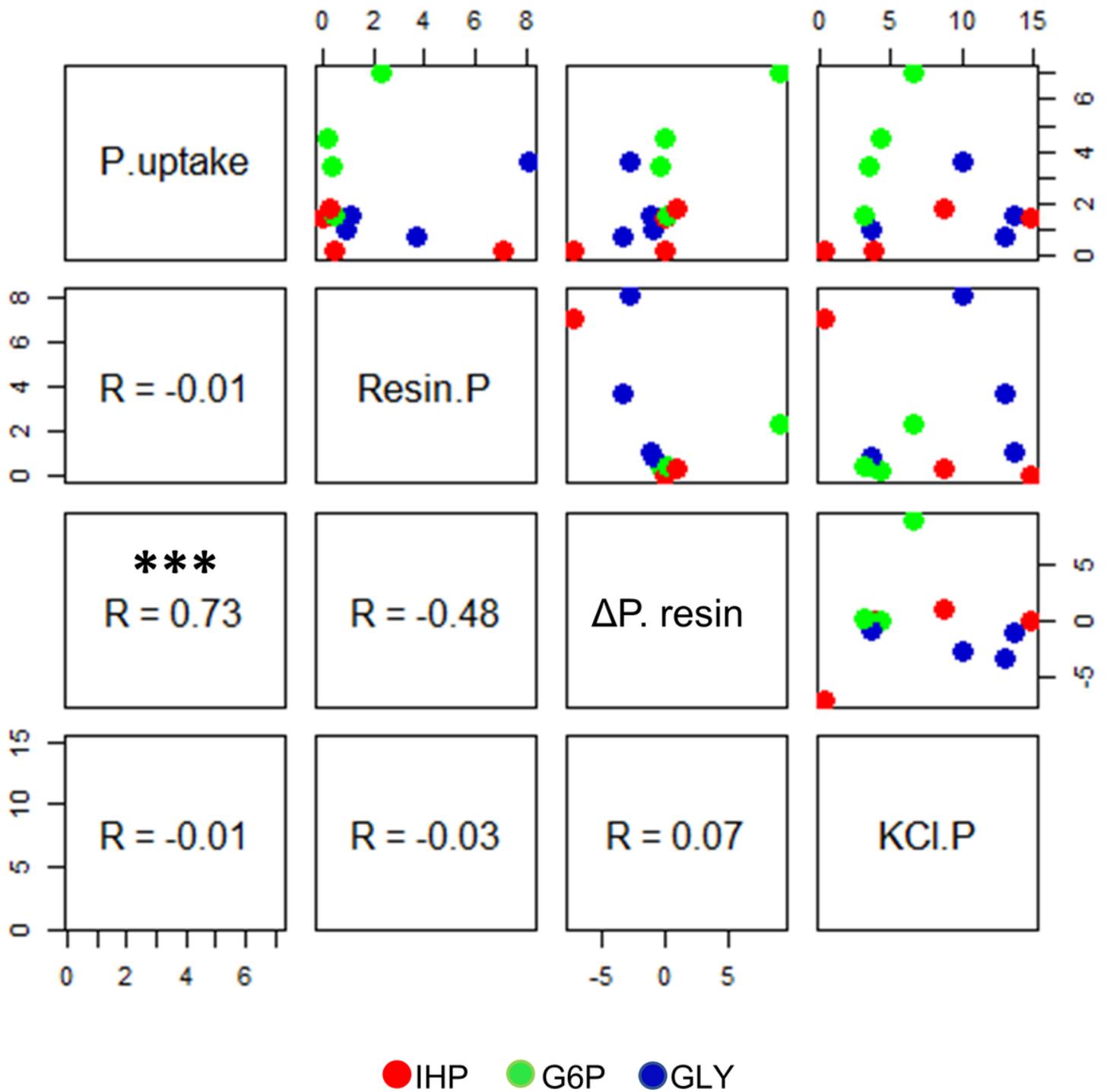


Figure 3

Correlations between P uptake and the different methods of P extraction. ΔP resin: Difference in resin P concentration between bulk soil and rhizosphere. KCl.P: KCl extracted P. Asterisks indicate significant differences between bulk soil and rhizosphere for each treatment (*, ** and ***: $p < 0.05$, 0.01 and 0.001)

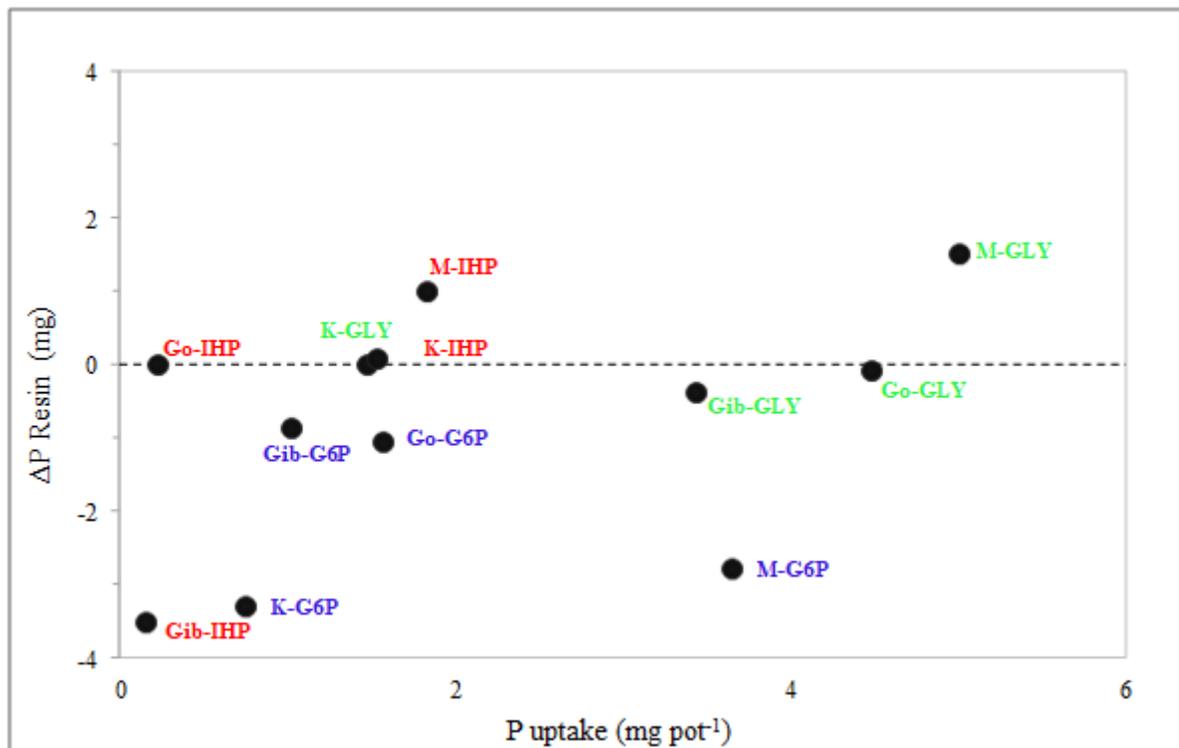


Figure 4

Relationship between Δ resin P (difference in resin P concentration between bulk soil and rhizosphere) and P uptake