European Journal of Soil Science

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European Journal of Soil Science

RESEARCH ARTICLE OPEN ACCESS

Organic Matter, and Particularly Phosphorylated Organic Matter, Coprecipitates Very Strongly With Aluminium

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Received: 12 December 2024 | **Revised:** 5 September 2025 | **Accepted:** 19 October 2025

Funding: This work was supported by the European Research Council (101043387).

Keywords: aluminium | coprecipitation | organic phosphorus | organo-mineral associations | soil organic carbon | soil organic matter | sorption

ABSTRACT

The aim of this study was to elucidate interactions between soil organic matter, inositol-hexaphosphate (IHP), aluminium (Al), and calcium (Ca) as well as four minerals (kaolinite, illite, smectite, and goethite) at low and high pH. For this purpose, we conducted experiments, in which we quantified the removal of soil-derived, natural organic matter (NOM) and IHP from the solution due to sorption and coprecipitation. The fraction of IHP in solution decreased due to Al addition to less than 2% of the initial amount, in all treatments (with and without minerals). The fraction of organic carbon (OC) of NOM in solution decreased due to Al addition in the absence of minerals to 12% of the initial amount and less strongly in the treatments with minerals to 39% of the initial amount. Aluminium addition decreased the fraction of OC of NOM in solution more strongly than the minerals, both at low and high pH. Addition of Ca and IHP also decreased the fraction of NOM in solution, particularly in the absence of minerals, but their effects were smaller than the effect of Al. Our finding that IHP decreased the fraction of NOM in solution supports the so-called anchor hypothesis stating that IHP can bind organic compounds to minerals and to other organic compounds. The effect of IHP on the fraction of NOM in solution was larger in the absence than in the presence of minerals, suggesting that IHP connects organic compounds to each other. Furthermore, the results show that IHP coprecipitates to a larger extent with Al than organic matter that has a very low phosphorus content. The results are important for understanding the architecture of organo-mineral associations, and specifically the role of organic phosphorus compounds therein, which is relevant for soil organic matter sequestration.

1 | Introduction

Soils store large amounts of organic carbon (OC), and the interaction of organic compounds with minerals is one of the main factors that stabilizes soil organic matter against decomposition (von Lützow et al. 2006; Kögel-Knabner et al. 2008; Kleber et al. 2015; Basile-Doelsch et al. 2020). Yet, the formation and the structure of the organo-mineral associations are not yet fully understood. Specifically, the role of metal cations and specific functional groups of the organic matter, such as the phosphate group, is not yet resolved (Jamoteau et al. 2023; Spohn 2024).

Organo-mineral interactions include adsorption and coprecipitation. Adsorption refers to the accumulation of organic compounds on mineral surfaces through various bond types. Coprecipitation involves several interaction processes (complexation, precipitation, and adsorption) between organic matter and metal species (Kleber et al. 2015). Interaction with minerals protects organic compounds against decomposition since it physically prevents exoenzymes from binding to the compounds to catalyze their decomposition. Further, sorption of organic compounds impedes uptake by microorganisms (von Lützow et al. 2006; Kögel-Knabner et al. 2008; Kleber et al. 2015).

Summary

- We studied the role of inositol-hexaphosphate (IHP) in organo-mineral interactions.
- Aluminium (Al) addition decreased IHP in solution to less than 2% of the initial amount.
- Al addition decreased natural organic matter (NOM) in solution to 12% of the initial amount.
- Thus, IHP coprecipitated to a larger extent than NOM with Al.
- Furthermore, IHP addition decreased NOM in solution, likely by binding it to minerals.

Sorption of soil organic matter depends on the charge density of organic compounds and minerals. Soil organic matter contains different functional groups that have pH-variable charge, such as carboxyl, hydroxyl, phenolic, amino, and phosphate groups. Most of these groups, including the phosphate group, are negatively charged when deprotonated, and the most abundant group in soil organic matter is the carboxyl group. The charge of oxides and hydroxides of iron, aluminium, silicon, and manganese is pH-variable, and it is mainly positive under acidic conditions. Clay minerals have both permanent negative charge and pH-variable charge, and the ratio of permanent-to-pH-variable charge varies among clay minerals and also depends on grain size. It is very small for kaolinite, very large for smectite, and intermediate for illite (Blume et al. 2015).

Multivalent metal cations play an important role in binding organic matter to mineral surfaces. A negatively charged functional group can bind to a negatively charged mineral through a multivalent metal cation that acts as a metal bridge (von Lützow et al. 2006; Kögel-Knabner et al. 2008; Kleber et al. 2015). In acidic soils, mainly aluminium (Al) acts as a bridge between negatively charged clay minerals and negatively charged organic functional groups (Kunhi Mouvenchery et al. 2012; Rasmussen et al. 2018; Yu et al. 2021). In addition, calcium (Ca) may be important for crosslinking organic matter to minerals, even in acidic soils (von Fromm et al. 2021; Rowley et al. 2023; Shabtai et al. 2023).

Dissolved organic compounds are usually aggregated in the soil solution due to their charge, hydrophobicity, and multivalent metal cations that connect different organic compounds (Kunhi Mouvenchery et al. 2012; Piccolo 2002, Piccolo 2001; Sutton and Sposito 2005; Schaumann 2006). Thus, the apparent molecular size of dissolved organic compounds is typically elevated, and several organic compounds act together as one supra-molecule (Piccolo 2002, 2001; Sutton and Sposito 2005). If these networks of organic matter and Al, Ca, iron (Fe), and silicon (Si) cations become very large, they can precipitate (Tamrat et al. 2019). Organo-mineral associations might mainly involve coprecipitation of organic compounds and Fe or Al, particularly in acidic soils (Jamoteau et al. 2023).

Besides nonspecific sorption (formation of outer-sphere complexes), organic compounds can also adsorb specifically, through ligand-exchange surface complexation (forming innersphere complexes). Ligand-exchange surface complexation refers to metal cations, mostly Fe and Al, replacing their coordinative OH or OH_2 ligand with another ligand, which can be an organic or inorganic ion (Stumm et al. 1980). Sorption of organic compounds to clay minerals and iron and aluminium oxides and hydroxides is pH-dependent. At low pH, mostly ligand-exchange surface complexation of carboxylates occurs, whereas at neutral and alkaline pH, nonspecific sorption of carboxylates predominates (Boily et al. 2000; Hwang and Lenhart 2008; Parikh et al. 2011). At low pH, a higher proportion of carboxylates is adsorbed to minerals than at elevated pH (Gu et al. 1996; Filius et al. 2000; Strahm and Harrison 2008).

Organic phosphorus (OP) compounds have a very high affinity to adsorb to minerals in soils (McKercher and Anderson 1989; Ognalaga et al. 1994; Martin et al. 2004; Celi and Barberis 2005; Berg and Joern 2006; Ruttenberg and Sulak 2011; Yan et al. 2014; Spohn 2024). OP compounds can adsorb to minerals through ligand-exchange surface complexation (innersphere complexation) via their phosphate moiety (Stumm et al. 1980; Goldberg and Sposito 1985; Ognalaga et al. 1994; Omoike et al. 2004; Cagnasso et al. 2010; Fang et al. 2012; Parikh et al. 2014; Chen and Arai 2019; Eusterhues et al. 2023). OP compounds comprise a multitude of phosphomonoesters and phosphodiesters that differ in their affinity to adsorb to mineral surfaces (Stewart and Tiessen 1987; Santoro et al. 2019). The most abundant OP compound in soils is the phosphomonoester inositol-hexaphosphate (IHP), also called phytate. It accounts for approximately 40% of the total soil OP (Darch et al. 2014; Deiss et al. 2018). IHP can adsorb to metal oxides through several of its phosphate groups at the same time (Ognalaga et al. 1994; Celi et al. 1999; Chen and Arai 2019, see also Figure 1).

Phosphate competes with organic compounds for binding sites on minerals (Spohn et al. 2022). Hence, an increase in the phosphate concentration of the soil solution can cause desorption of organic compounds (Kaiser and Zech 1999; Zhang and Zhang 2010; Bonifacio et al. 2013; Scott et al. 2015; Spohn and Schleuss 2019; Spohn et al. 2022). Yet, it could be that OP compounds with multiple phosphate groups, such as IHP, form organo-organic complexes and also bind organic matter to minerals (Spohn 2024), as shown for IHP and proteins (Cheryan and Rackis 1980). Specifically, IHP might adsorb to a mineral surface with up to four phosphate moieties (Ognalaga et al. 1994; Celi et al. 1999; Chen and Arai 2019) and to other organic compounds through the other phosphate moieties. Thus, IHP might bind organic matter to a mineral surface (Figure 1), or link several organic compounds with each other (Spohn 2024).

The aim of this study was to elucidate interactions of soil-derived, natural organic matter (NOM) with aluminium (Al), calcium (Ca), and IHP as well as four different minerals (three clay minerals and one iron oxide) at low and high pH (caused by a NOM solution whose pH was adjusted to pH 4.9 or 6.8, respectively). For this purpose, we conducted an experiment, in which we quantified removal of OC of NOM and IHP due to sorption and coprecipitation. We tested the following four hypotheses.

H1. *The addition of Ca, Al, or IHP to a NOM solution removes OC of NOM from* the *solution in both the presence and absence*

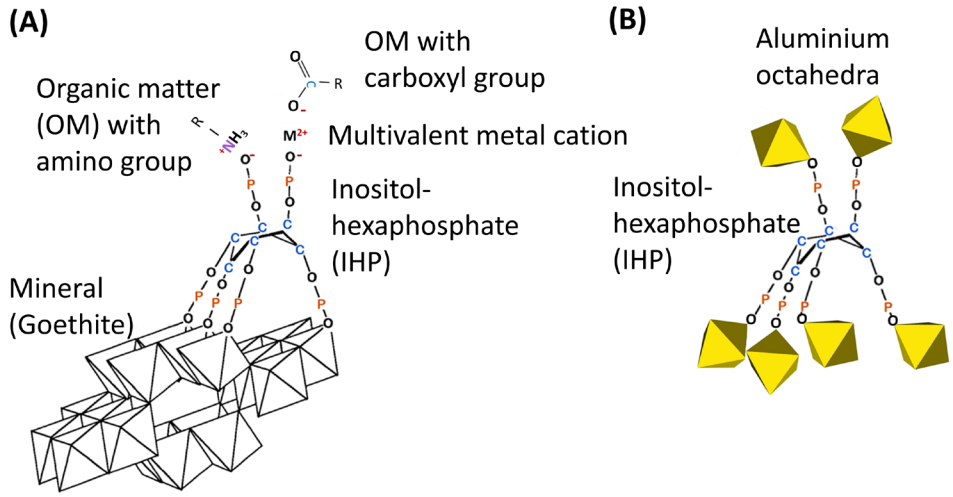

FIGURE 1 | Conceptual figure showing interactions between inositol hexaphosphate (IHP) and soil minerals. Panel (A) illustrates the anchor hypothesis, which states that IHP binds to minerals and at the same time to organic matter (OM) either via an amino group of the OM or a carboxyl group of the OM and a multivalent metal cation (modified after Ognalaga et al. 1994 and Spohn 2024). Panel (B) illustrates co-precipitation of IHP and aluminium due to specific adsorption of the phosphate groups of IHP to aluminium octahedrons.

of minerals (because Ca, Al, and IHP connect organic matter to minerals and in addition, cross-link organic compounds, forming supra-molecules that precipitate).

H2. *A larger proportion of IHP than of NOM is removed from solution due to the addition of minerals and metal cations (because OP compounds have a very high affinity to adsorb to mineral surfaces and they might also have a high affinity to co-precipitate with metal cations).*

H3. *The combined addition of IHP and either Ca or Al leads to a particularly high removal of OC from solution in the treatments with clays (because Ca and Al bridge negative charges, and thus allow IHP to bind to negatively charged clay minerals and at the same time to other organic compounds).*

H4. *Removal of OC of IHP from solution is higher in the treatments with goethite than in the treatments with clay minerals, particularly at low pH (due to the charge of goethite, which is positive under acidic conditions and increases with decreasing pH).*

We included Al in the experiment because it was recently found that the Al concentration in Swedish forest soils correlates with the soil OC concentration (Spohn and Stendahl 2024). Furthermore, we included Ca, because Ca has recently been suggested to play a role in stabilizing soil organic matter (Rasmussen et al. 2018; Rowley et al. 2023; Shabtai et al. 2023).

2 | Material and Methods

2.1 | Soil Organic Matter and Minerals

The soil organic layer of a mixed forest in Uppsala, Sweden (59.81°N, 17.67°E) was sampled in spring 2023. The forest is a mixed pine-spruce forest (*Pinus sylvestris* and *Picea abies*); the soil is classified as a podzol according to the World Reference Base for Soil Resources (IUSS Working Group WRB 2015), and the organic layer had a depth of 12 cm. The site was chosen because it is representative of forests in central Sweden (Spohn and Stendahl 2024). One sample of the organic layer was taken down to a depth of 10 cm in the organic layer using a shovel. Twigs and mosses were removed from the organic layer material. Subsequently, 200 g of moist organic layer material was extracted in 800 mL of water for 24 h on a horizontal shaker-incubator (New Brunswick Innova 42R) at 6°C. The soil extract was first passed through a Whatman filter with 10 μm pore size and subsequently it was filtered through a cellulose membrane filter (Merck) with a pore size of 0.22 μm using vacuum filtration (which excludes bacteria due to the small pore size). The filtered extract (called NOM or NOM solution from here on) had the following properties: pH 4.9, 33.7 mg l^{-1} C, 2.1 mg l^{-1} N, 0.17 mg l^{-1} P, 1.88 mg l^{-1} Ca, and 0.24 mg l^{-1} Al. The molar C:N ratio was 18.7.

The experiment involved the four minerals: kaolinite, illite, smectite, and goethite. The kaolinite (KGa-1) and the smectite (STx-1) are reference clays of The Clay Minerals Society, and were purchased from Source Clays (Chantilly, VA, United States). They are very well characterized (Chipera and Bish 2001) and used in many studies. The illite (Illite du Puy, IDP) is also a model clay system and well characterized (Asaad et al. 2022). The illite was obtained from Argile du Velay (Saint-Paulien, France). The mineral called kaolinite here is a relatively pure kaolinite with 96% kaolinite (Chipera and Bish 2001), the mineral called illite here contains 81.1% illite, 6.1% K-feldspar, 5.3% calcite, 4% kaolinite, and 1.5% quartz (Asaad et al. 2022), while the mineral called smectite here contains 68% smectite, 30% opal-C/CT, and 2% quartz (Chipera and Bish 2001). Kaolinite is low in defects and has a cation exchange capacity of 3.0 meq 100 g^{-1} (Borden and Giese 2001). The smectite has a cation exchange capacity of 89 meq 100 g^{-1} (Borden and Giese 2001). The illite has a cation exchange capacity of 21.1 meq 100 g^{-1} (Asaad et al. 2022). The iron oxide goethite ($FeHO_2$) was purchased from Sigma Aldrich (number 71063). The goethite has a point of zero charge of 7.8 (Tsang et al. 2013). Kaolinite, illite, smectite, and goethite have a specific surface area of 10, 123, 84, and 8 m^2 g^{-1}, respectively (for further characteristics see Table S1).

2.2 | Experimental Design and Analysis

We conducted the same experiment with the NOM solution at low and high pH. In the first experiment, the initial pH of the NOM solution (pH 4.9) was not manipulated prior to the experiment, while in the second experiment, the pH of the solution was set to 6.8 by slowly adding NaOH to the NOM solution until a stable pH of 6.8 was reached before the start of the experiment.

All experiments were conducted with NOM and involved the four minerals (kaolinite, illite, smectite, and goethite). For each mineral, there were the following treatments: no ion addition, Ca addition, Al addition, IHP addition, Ca + IHP addition, and Al + IHP addition. Furthermore, there were four treatments without minerals, namely no ion addition, Ca addition, Al addition, and IHP addition. There were four replicates for every treatment.

All experiments were conducted at 6°C in order to minimize biotic activity. The NOM solution was allowed to reach 6°C before the start of the experiment. For the experiment, 45 mg of each mineral were weighed into centrifugation tubes. Each experiment was started by filling 45 mL of the cooled NOM solution into the centrifugation tubes (which, depending on the treatment, contained or did not contain one of the minerals). Immediately afterwards, Ca, Al and IHP were added to the solution, depending on the treatment. Specifically, Ca was added in 0.1 mL of an 8.4×10^{-2} M solution, Al was added in 0.1 mL of an 8.4×10^{-2} M solution, IHP was added in 0.1 mL of a 1.4×10^{-2} M solution. Ca was added as calcium chloride dihydrate ($CaCl_2.2H_2O$, 147.01 g mol^{-1}, Merck), Al was added as aluminium chloride hexahydrate ($AlCl_3.6H_2O$, 241.43 g mol^{-1}, EMD Chemicals), and IHP was added as phytic acid sodium salt hydrate ($C_6H_{18}O_{24}P_6.Na.H_2O$, 660 g mol^{-1}, Sigma-Aldrich). For a similar experimental design, see Ruttenberg and Sulak (2011). Directly after filling the centrifugation tubes, they were placed in an incubator-shaker at 6°C (New Brunswick Innova 42R). After 1 h, the tubes were centrifuged for 15 min at 5200 G (Beckman Coulter—Allegra X15R). We determined DOC as well as total P, Al, Ca, and pH in the supernatants.

The DOC concentration was determined using a TOC analyzer (multi-N/C 2100, Jena Analytics, Germany). P, Al, and Ca were determined using ICP-OES (Perkin Elmer Avio 200), and pH was measured using a pH electrode (LE438 sensor, Mettler Toledo FiveEasy F20).

2.3 | Calculations and Statistics

We calculated the amount of OC of IHP in solution based on the P concentration and the molar C:P ratio of IHP (which is 1). We corrected the measured OC concentration in solution for OC from IHP, in all treatments involving IHP. This was possible because the NOM solution contained only negligible amounts of phosphorus, much less than what was added in the form of IHP (see above). The initial molar C:P ratio of the dissolved organic matter in the treatments with IHP was 21.5. Furthermore, we calculated the fraction of OC of NOM in solution for all treatments, and the fraction of OC from IHP for all treatments involving IHP. In addition, we estimated the molar C:P ratio of the precipitates based on the removal of C and P from the solution. To test our hypotheses, we compared different treatments by student's *t* test in R, and we considered $p < 0.05$ as the threshold for significance (R Core Team 2021).

3 | Results

3.1 | OC of NOM

Aluminium significantly decreased the fraction of OC of NOM in solution in all treatments (Figure 2). In the Al treatment at low pH, in the absence of minerals, only 12% of OC remained in solution, whereas in the Al treatments at low pH with minerals, between 22% and 39% of OC remained in solution. In the Al treatments at high pH, in the absence of minerals, 56% of OC remained in solution. At high pH, the effect of Al in the kaolinite treatment was very similar to the effect of Al in the absence of minerals (also 56%), whereas, the other three minerals slightly diminished the effect of Al, and between 65% and 66% of OC remained in solution in these treatments (Figure 2).

The effect of Ca on the fraction of OC in solution was much smaller than the effect of Al (Figure 2). In the absence of minerals, Ca significantly decreased the fraction of OC remaining in solution at low pH (down to 28% of the initial amount) and at high pH (down to 86% of the initial amount, Figure 2). In contrast, in the treatments with minerals, Ca only had a minor effect on the fraction of OC in solution (Figure 2). The effect of Ca on OC in solution was significant in most mineral treatments, but not in the treatments with illite and kaolinite at low pH (Figure 2).

IHP decreased the fraction of OC of NOM in solution substantially at low pH in the absence of minerals (down to 48% of the initial amount; Figure 2). In treatments with minerals, the negative effect of IHP on OC in solution was statistically significant in the smectite treatment at low pH, and in the kaolinite, illite, and goethite treatments at high pH (Figure 2). The size of the effect of IHP addition on the fraction of NOM in solution was very similar to the effect of Ca (Figure 2).

The combined addition of Al and IHP decreased the fraction of OC in solution significantly less than single Al addition, at high pH (Figure 2B). In contrast, at low pH, the combined addition of Al and IHP decreased the fraction of OC in solution significantly more than single Al addition in the kaolinite treatment. Similarly, the combined addition of IHP and Ca decreased OC in solution more compared to single Ca addition, in the treatments with kaolinite in both pH treatments (Figure 2).

At high pH, the fraction of OC of NOM remaining in solution varied between 92% and 100% of the initial amount in the four mineral treatments without ion addition (Figure 2B), and it did not differ significantly between goethite and the clay minerals (Figure 1). However, at low pH, the fractions of OC remaining in solution were much lower than at high pH and differed much more and statistically significantly among the mineral treatments (Figure 2A). The fraction of OC remaining in solution at low pH decreased in the order kaolinite (59%) > illite (49%) > goethite (32%) > smectite (30%) treatment (Figure 2B).

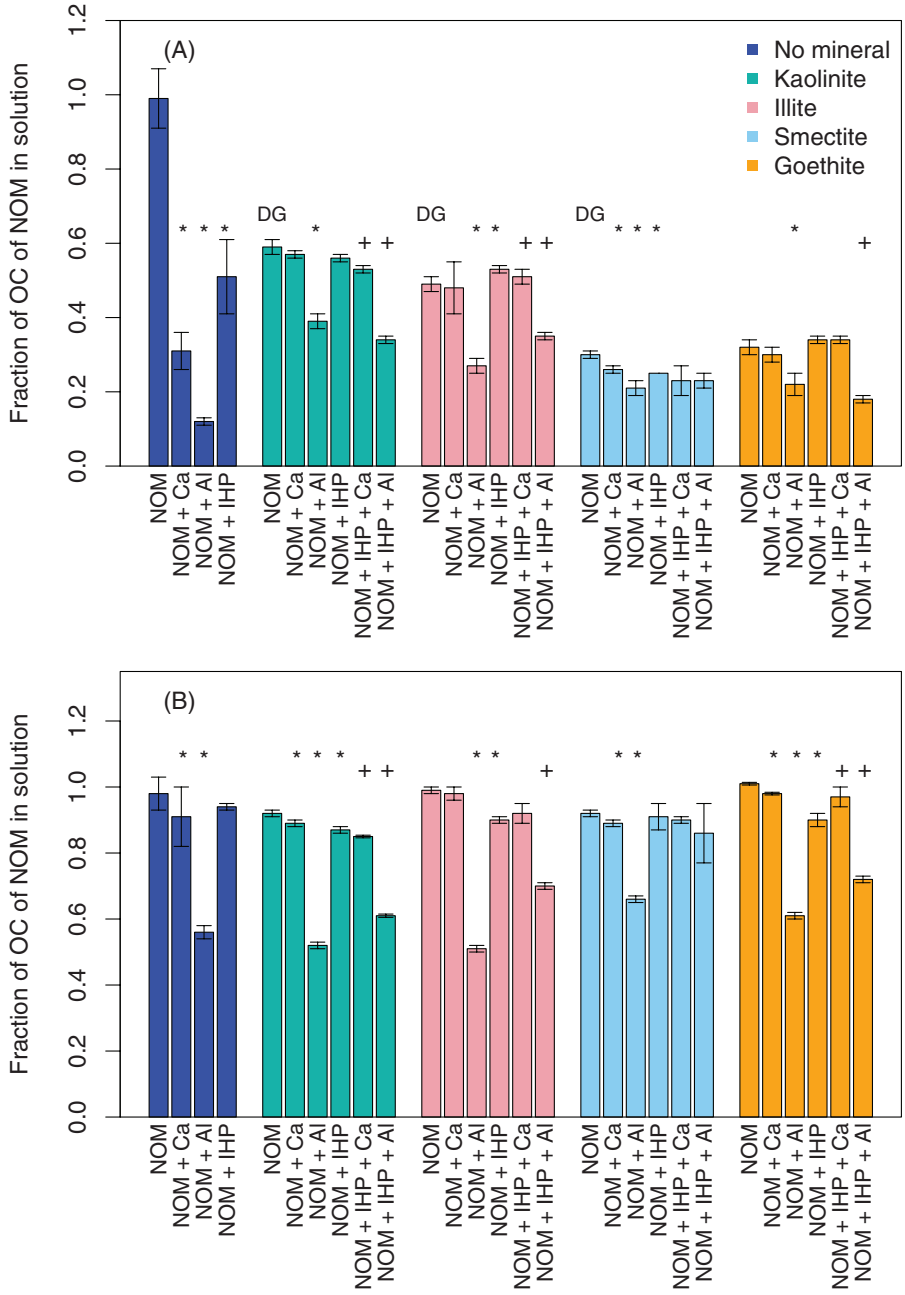

FIGURE 2 | The fraction of organic carbon (OC) of soil-derived, natural organic matter (NOM) in solution at low pH (A) and high pH (B) depending on minerals (kaolinite, illite, smectite, and goethite) as well as calcium (Ca), aluminium (Al) and inositol-hexaphosphate (IHP) addition. In the treatments including IHP, the amount of OC was corrected for OC of IHP to show only OC of NOM. Columns show means and error bars show standard deviations, calculated across four replicates. An asterisk (*) indicates that a single ion addition treatment (+Ca, +Al, or + IHP) caused a significantly different fraction of OC in solution compared to the control treatment (NOM, no ion addition), tested according to H1. A cross (+) indicates that the combined ion addition +IHP + Ca or + IHP + Al caused a significantly different fraction of OC in solution compared to the +Ca or the +Al treatment, respectively, tested according to H2. H1 and H2 were tested separately for all mineral and pH treatments. The letters "DG" indicate that the fraction of OC in solution is significantly different compared to the goethite treatment, and this was tested for all NOM treatments (without ion addition). The detailed results of the statistical comparisons are given in the Supporting Information Tables S2–S6.

3.2 | OC of IHP

Aluminium had a much larger effect on IHP than on NOM in solution, both at high and low pH (Figure 3). The fraction of OC of IHP in solution varied between 0.2% and 1.8% of the initial amount at low pH (Figure 3A) and between 0.6% and 1.2% of the initial amount at high pH in the four mineral treatments (Figure 3B).

Furthermore, the four minerals removed a larger proportion of OC of IHP than of OC of NOM from solution (compare Figures 2 and 3). In the illite treatment, OC of IHP was most strongly decreased compared to the other mineral treatments both at low pH (only 10% of the initial amount remained in solution) and at high pH (only 11% of the initial amount remained in solution). The second lowest removal of OC of IHP was found in the goethite treatment both at low pH (16% of the initial amount

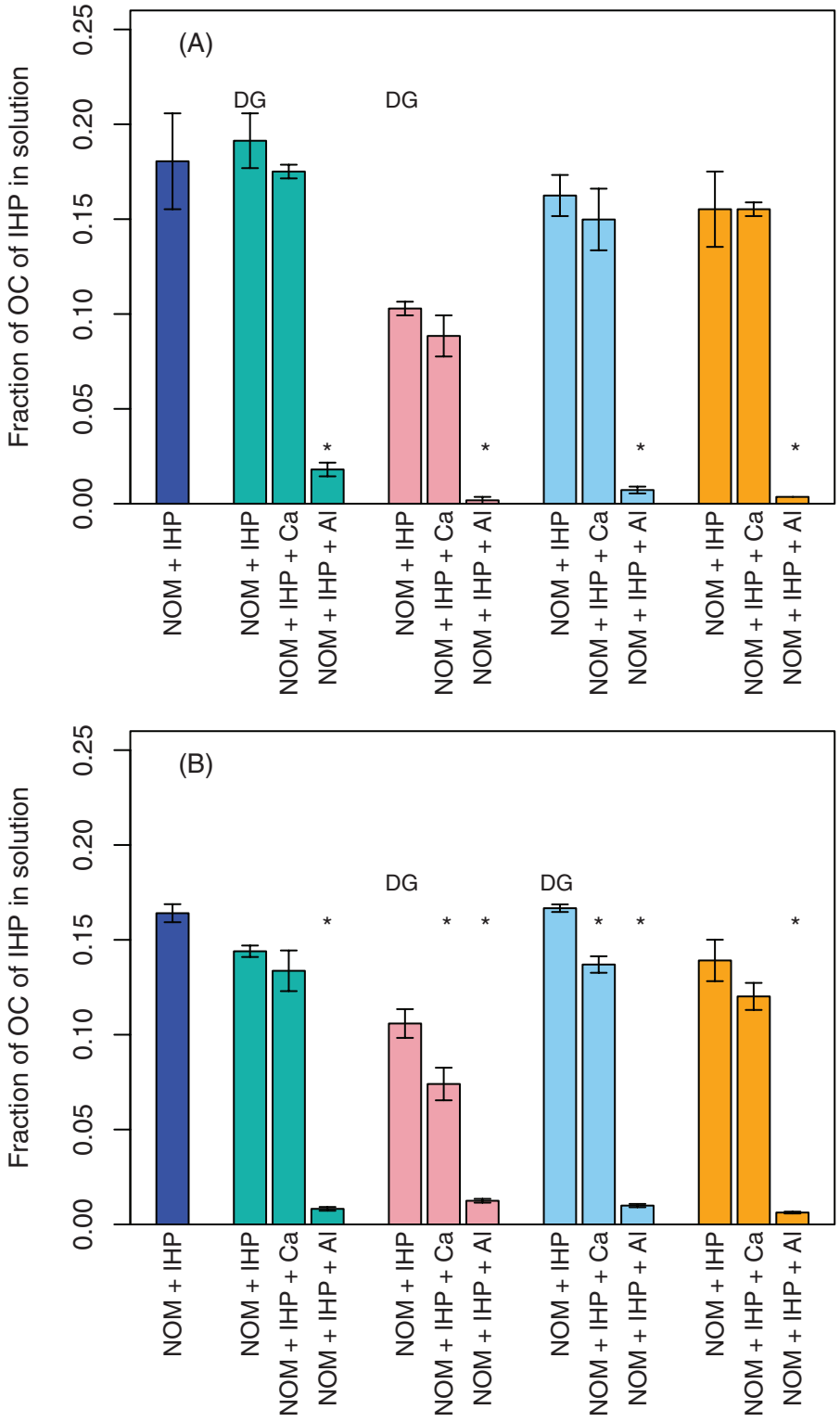

FIGURE 3 | The fraction of organic carbon (OC) of inositol-hexaphosphate (IHP) in solution at low pH (A) and high pH (B) depending on minerals (kaolinite, illite, smectite, and goethite) as well as calcium (Ca) and aluminium (Al) addition. Columns show means and error bars show standard deviations, calculated across four replicates. Please notice that the scale on the y-axis differs from the one in Figure 2. An asterisk (*) indicates that the combined ion addition +IHP + Ca or + IHP + Al leads to a significantly different fraction of OC of IHP in solution compared to the +IHP treatment, tested separately for all mineral and pH treatments. The letters "DG" indicate that the fraction of OC of IHP in solution is significantly different compared to the goethite treatment and this was tested for all +IHP treatments without cation addition, according to H4. The detailed results of the statistical comparisons are given in the Supporting Information Tables S7–S8.

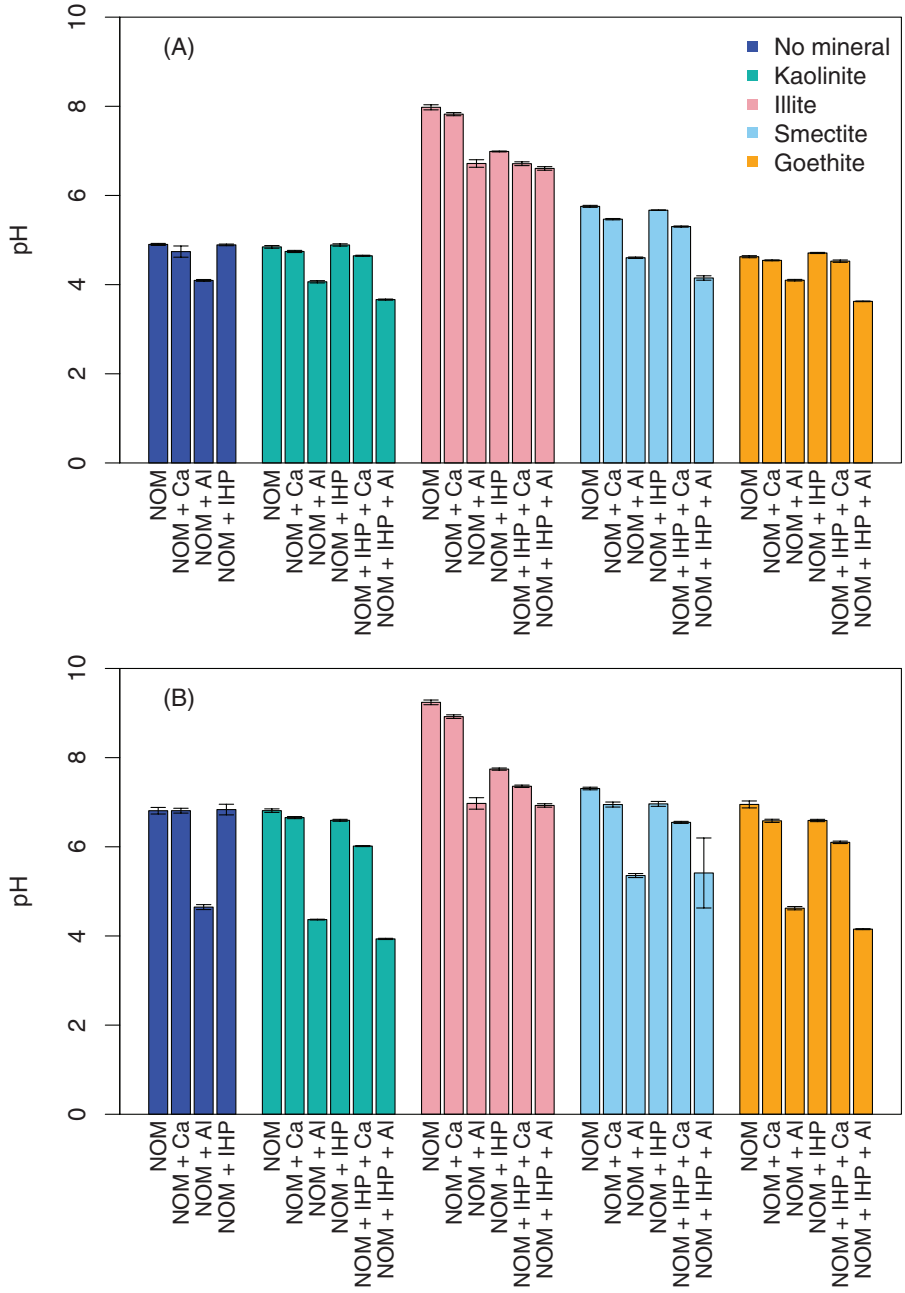

FIGURE 4 | The pH of a natural organic matter (NOM) solution in the low pH treatment (A) and the high pH treatment (B) depending on minerals (kaolinite, illite, smectite, and goethite) as well as calcium (Ca), aluminium (Al) and inositol-hexaphosphate (IHP) addition. Columns show means and error bars show standard deviations, calculated across four replicates.

remained in solution) and at high pH (17% of the initial amount remained in solution). Thus, the removal of OC of IHP from the solution was similar in the low and high pH treatments.

The molar C:P ratio of precipitated organic matter ranged between 6 and 12 in the kaolinite treatments, and between 2 and 8 in the other mineral treatments at high pH. The initial molar C:P ratio of the dissolved organic matter in the treatments with IHP was 21.5.

3.3 | pH

Aluminium addition decreased the pH in all treatments (Figure 4). Furthermore, illite and, to a lesser extent, smectite increased the pH compared to the treatments without minerals (Figure 4). Specifically, the pH in the illite and smectite treatments was 8.0 and 5.8, respectively, in the low pH experiments (Figure 4A), and 9.2 and 7.3, respectively, in the high pH experiments (Figure 4B).

4 | Discussion

4.1 | The Effect of Ca, Al, and IHP on NOM in Solution

We found support for H1 stating that the addition of Ca, Al, or IHP decreases the concentrations of OC in solution (Figure 2). The addition of Al, Ca, and IHP decreased OC in solution in

the absence and presence of minerals, particularly at low pH (Figure 2). The reason for the decrease in OC in the absence of minerals is likely that Al, Ca, and IHP connected different organic compounds. Consequently, the organic compounds act together as a supramolecule with an elevated (apparent) molecular size. This caused coprecipitation of organic matter in our experiment due to centrifugation (Masion et al. 2000; Schaumann 2006; Kunhi Mouvenchery et al. 2012; Tamrat et al. 2019; Jamoteau et al. 2023). IHP interacts strongly with the positively charged amino groups of organic matter (Cheryan and Rackis 1980; Selle et al. 2012). In addition, it could be that NOM binds to the phosphate groups of IHP through carboxyl groups and multivalent metal cations (see Figure 1). Our finding that IHP decreased the fraction of NOM in solution more strongly in the absence than in the presence of minerals (Figure 1A) suggests that IHP can connect different organic compounds (Piccolo 2001; Piccolo 2002; Sutton and Sposito 2005; Schaumann 2006; Kunhi Mouvenchery et al. 2012).

The effect of Al on OC in solution was particularly strong (Figure 2), which is in accordance with previous studies. For instance, it was shown that NOM strongly coprecipitated with Al, forming flocs, and that Al oxide monomers were the predominant Al species in aged flocs (Masion et al. 2000). Furthermore, it was reported that in solutions of acidic forest soils, up to 90% of the organic matter coprecipitated with Al (Scheel et al. 2008). In accordance with these findings, a recent study suggested that soil organo-mineral complexes largely consist of coprecipitates of organic matter and Fe, Si, and Al oxides that are structured in a loose, irregular 3-dimensional network (Tamrat et al. 2019). In addition, it was found that OC concentrations were correlated with exchangeable Al across a large number of acidic forest soils, and these correlations were particularly strong in soils with sandy texture, where organo-organo interactions might be particularly important for organic matter stabilization (Spohn and Stendahl 2024). Furthermore, a very strong co-localization of Al and OC in an Andosol was recently reported, suggesting that in acidic soils, organo-mineral associations mainly involve coprecipitation of organic compounds and Fe and Al (Jamoteau et al. 2023).

The effect of Al on the fraction of OC of NOM in solution in the absence of minerals was larger than the effect of minerals (without added ions), both at low and high pH (Figure 2). This underlines the high affinity of the organic matter to coprecipitate with Al. The reason for the high affinity of both IHP and NOM to coprecipitate with Al is most likely that the Al forms Al oxides in solution by hydrolysis, as indicated by the decrease in pH in the Al addition treatments (Figure 4). NOM and IHP can likely bind to the Al oxides specifically, that is, through inner sphere complexation via carboxyl and phosphate groups, respectively, which causes the organic matter to coprecipitate with the Al oxides (see Figure 1B). The results suggest that coprecipitation of organic matter with Al oxides might be very important for the formation of organo-mineral associations in acidic soils with high Al concentration. Our results are particularly remarkable given that the minerals used in the experiment had not previously been in contact with organic matter, and thus should be more reactive than minerals in soils. Thus, in soils, the effect of Al might outperform the effect of minerals on organic matter stabilization even more strongly than in our experiment.

The fraction of OC of NOM in solution in the Al treatments was smaller in most mineral treatments than in the absence of these minerals, at low pH (Figure 1B), indicating that a part of the Al adsorbed to the minerals, and thus did not coprecipitate with the NOM.

The effect of Ca on OC in solution was much smaller than the effect of Al, particularly in the treatments involving minerals (Figure 2). The reason for this is likely that Ca cations in contrast to Al cations do not form oxides in the soil solutions. The lower effect of Ca than of Al cations on OM is in accordance with previous studies. For example, a recent study showed that organic matter was positively correlated with exchangeable Al but not with exchangeable Ca across a large number of acidic forest soils (Spohn and Stendahl 2024). A smaller relationship between Ca and organic matter than between Al and organic matter was recently also reported for Andosols (Jamoteau et al. 2023). Furthermore, the small effect of Ca observed here is in accordance with a recent study demonstrating that Ca addition reduced soil microbial respiration by only 4% (Shabtai et al. 2023).

Our finding that IHP removed OC from the soil solution in the absence and presence of minerals supports the so-called anchor hypothesis stating that IHP can bind organic compounds to other organic compounds or to minerals through its multiple, charged phosphate moieties (Spohn 2024; Figure 1). The size of the effect of IHP on the fraction OC of NOM in solution was similar to the effect of Ca (Figure 2).

Taken together, we found that the effect of Al on the fraction of OC of NOM in solution in the absence of minerals was larger than the effect of minerals (without added ions), emphasizing the high affinity of organic matter to coprecipitate with Al. The results indicate that coprecipitation of organic matter and Al might be more important than adsorption for the formation of organo-mineral associations, under acidic conditions. Furthermore, we found support for the so-called anchor hypothesis, and the size of the effect of IHP on the fraction of NOM in solution was very similar to the size of the effect of Ca.

4.2 | IHP in Comparison to NOM

In accordance with H2, we found that the addition of Al had an even stronger effect on the fraction of OC of IHP than on the fraction of OC of NOM in solution. Less than 2% of the OC of IHP remained in solution in the mineral treatments with Al, both at low and high pH (Figure 3). These results underline the high affinity of IHP to coprecipitate, a process that might thus be very important for the stabilization of IHP against microbial decomposition in soils. Our results are in accordance with studies reporting a strong interaction of OP and Al. For example, Giesler et al. (2005) studied phosphorus dynamics in forest soils with high organic matter contents and high native amounts of Al and Fe and found that OP strongly coprecipitated with Al and Fe. Furthermore, Mikutta et al. (2011) examined the chemical fractionation of organic matter during reactions with dissolved and colloidal Al species. They reported that OP compounds were preferentially bound during both adsorption and coprecipitation processes compared to nonphosphorylated organic

compounds. Furthermore, Yan et al. (2014) investigated the adsorption of various OP compounds to three aluminium (oxyhydr)oxides (short-range order $Al(OH)_3$, boehmite, and α-Al_2O_3) and observed that the amounts of OP adsorbed increased with decreasing crystallinity of the minerals. The high affinity of OP compounds to precipitate with Al oxides (compared to nonphosphorylated organic compounds) has also been described in studies about the removal of OP compounds from wastewater (Rott et al. 2017; Liu et al. 2018). In addition, the high affinity of OP compounds to precipitate with Al oxides is used in a novel technique that allows isolating OP from other organic compounds to measure its isotopic signature (Tian and Spohn 2025).

Ca had only a very small effect on the fraction of OC of IHP in solution, and the effect was only significant in the treatments with illite and smectite at high pH (Figure 3). This is in accordance with previous studies reporting a less strong relationship between Ca and organic matter than between Al and organic matter (Jamoteau et al. 2023; Spohn and Stendahl 2024).

The result that the OP compound IHP adsorbed more strongly to the four minerals than NOM is in accordance with studies about competitive sorption of OC and OP (for a review see Spohn 2024). For instance, Cao et al. (2011) determined the affinity constant of OC and OP to adsorb to three minerals. They found that the affinity constant was larger for OP than for OC by a factor of 648, 16, and 7 in experiments with montmorillonite, kaolinite, and goethite, respectively. Omoike and Chorover (2006) determined the affinity constants of OC and OP to adsorb to goethite to be larger for OP than for OC by a factor of 714–2397. Similarly, Lin et al. (2016) and Swenson et al. (2015) found that OP adsorbed to a larger extent than nonphosphorylated organic compounds. Yet, the strong preferential coprecipitation of OP compounds with Al compared to nonphosphorylated organic matter has not been described in detail yet (but see Mikutta et al. 2011).

Taken together, our results show that the OP compound IHP interacts more strongly with Al than nonphosphorylated organic compounds. This has important implications for understanding the architecture of organo-mineral associations and the role of OP compounds therein. The results might suggest that OP compounds are more strongly protected against decomposition than nonphosphorylated compounds due to their high affinity to precipitate with Al.

4.3 | The Combined Effect of IHP and Metal Cations on NOM in Solution

Support for H3 (that the addition of IHP and either Ca or Al leads to particularly high removal of OC of NOM from the solution in the treatments with clays) was only found for kaolinite at low pH (Figure 2). However, this negative effect of combined IHP and metal cation addition on OC in solution was small. The fact that we found little support for H3 seems to indicate that NOM adsorbs mostly directly to IHP, for example through amino groups and not through carboxyl groups of the NOM and multivalent metal cations (see Figure 1). This explanation is supported by studies reporting strong interactions of IHP and amino acids and proteins (Cheryan and Rackis 1980; Selle et al. 2012). In addition, it could also be that the concentration of multivalent metal cations in our experiment did not limit NOM binding to IHP in the mineral treatments because the minerals also contain Ca.

Against H3, we observed that the combined addition of Al and IHP significantly and consistently increased OC in solution compared to single Al addition at high pH in all four mineral treatments (Figure 2). This indicates that at high pH, IHP interacted with Al in a way that decreased the interaction of Al and NOM. It seems likely that IHP coprecipitated with Al, which decreased coprecipitation of Al and NOM. This interpretation is supported by the strong coprecipitation of IHP and Al (see Section 4.2). Our finding that IHP prevents organic compounds from coprecipitating with Al is important for understanding the formation of organo-mineral associations because it indicates that the stoichiometry of organic matter, and specifically its C:P ratio, affects coprecipitation of organic matter through the phosphate group.

4.4 | The Effect of pH on Organo-Mineral Interactions

The effect of Al, Ca, and IHP on OC in solution was larger at low than at high pH, which is very likely due to the fact that the pH influences the binding form of organic matter. At low pH, mainly ligand-exchange surface complexation of carboxylates occurs, whereas at neutral and alkaline pH, nonspecific sorption of carboxylates dominates (Boily et al. 2000; Hwang and Lenhart 2008; Parikh et al. 2011). Thus, at low pH, a higher proportion of carboxylates is typically adsorbed than at elevated pH (Gu et al. 1996; Filius et al. 2000; Strahm and Harrison 2008). In addition, the negative charge of soil organic matter increases with increasing pH, and therefore more cations are required to promote organic matter flocculation at high pH. Furthermore, the pH also affects the speciation of Al and the protonation of the oxides, which likely influences organo-mineral interactions.

Removal of OC of IHP from the solution due to minerals and ions was less pH-dependent than the removal of OC of NOM from the solution (compare Figures 2 and 3). The reason for this is likely that the binding form of carboxylates is pH-dependent, whereas OP compounds bind via specific sorption, that is, ligand exchange surface complexation, which is less dependent on the pH (Omoike et al. 2004; Cagnasso et al. 2010; Fang et al. 2012; Parikh et al. 2014; Chen and Arai 2019).

4.5 | The Effect of Different Minerals and pH

The comparison of the different mineral treatments has to be considered with some caution since we cannot fully disentangle the effect of the minerals and the mineral-induced pH changes based on the design of our experiment. Of all minerals, illite, and not goethite, decreased the amount of OC of IHP in solution most strongly (Figure 3), in contrast to H4. The main reason for this is likely the relatively high specific surface area of illite that is larger than the specific surface of goethite (see Material and Methods, and Table S1). In addition, illite has sorption sites that have a high affinity to adsorb phosphorus (Guo et al. 2024). Furthermore, of all minerals, smectite removed the largest

proportion of OC of NOM from solution (Figure 1). The most likely reason for this seems to be the high cation exchange capacity of the smectite (see Material and Methods and Table S1), which allows a large amount of organic compounds to adsorb to the mineral either through positively charged functional groups or via metal cations. In addition, smectite also has interlayer space into which organic matter can be incorporated.

4.6 | Limitations of the Experiment

It needs to be considered that the present experiment, as every experiment, is based on specific materials and conditions that affect the results. We choose to work with a nutrient-poor NOM solution (derived from a nutrient-poor organic layer of a forest soil) because this allowed us to distinguish between NOM and IHP. However, the fact that the NOM is not only phosphorus-poor but also nitrogen-poor (molar C:N ratio of 18.7), likely affected the results. Specifically, the low number of amino groups of the NOM might give the NOM a low affinity to adsorb to IHP or to co-precipitate with IHP since NOM can bind to IHP through its amino groups (Figure 1). Thus, our choice to work with a nitrogen-poor SOM solution might have caused the small effect of IHP addition on the fraction of NOM in solution (Figure 3). Future studies should explore the interactions of IHP and nitrogen-rich organic matter, such as amino acids. Furthermore, we only choose to work with four (characterized) minerals but cannot make inferences about others. In addition, we choose to work with two different pH ranges, but did not study alkaline conditions. Thus, we cannot make inferences about those, and we cannot fully disentangle the effect of the mineral and the mineral-induced pH change based on the design of our experiment. Furthermore, it also needs to be considered that the concentrations of Al, Ca, and IHP in the experiments were relatively high compared to soil solution.

5 | Conclusions

We found support for the hypothesis that the addition of Ca, Al, or IHP to a solution of NOM removes NOM from the solution in both the presence and absence of minerals. Specifically, IHP removed NOM from the soil solution to a similar extent as Ca. This is likely because IHP can bind organic compounds to minerals and to other organic compounds, similarly to the multivalent metal cations. The effect of IHP on the fraction of NOM in solution was particularly large in the absence of minerals, suggesting that IHP plays an important role in connecting organic compounds in the absence of minerals. Furthermore, we also found support for H2 stating that a larger proportion of IHP than of NOM is removed from the solution due to the addition of minerals and metal cations, particularly with respect to Al addition. Our study shows that the effect of Al on the fraction of OC of NOM in solution was larger than the effect of minerals, both at low and high pH. This underlines the high affinity of the organic matter, and particularly of IHP, to coprecipitate with Al, under the conditions of our experiment. The results suggest that coprecipitation with Al is an important process for the formation of organo-mineral associations. Furthermore, our results show that the OP compound IHP interacts more strongly with Al than nonphosphorylated organic compounds. Thus, one could speculate that IHP is more strongly protected against decomposition than nonphosphorylated compounds due to its high affinity to precipitate with Al. Our results are important for understanding the architecture of organo-mineral associations. Future studies should explore to what extent OP that has precipitated with Al is protected against enzymatic hydrolysis, and to which extent biota can mobilize OP that precipitated with Al, for instance through the release of chelators or oxidative enzymes.

Author Contributions

Yaana Bruneel: investigation. **Marie Spohn:** conceptualization, funding acquisition, writing – original draft, supervision, project administration, writing – review and editing.

Acknowledgements

We thank Hui Liu and Mina Spångberg for technical assistance. The European Research Council is acknowledged for funding (grant no. 101043387).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Properties and chemical composition of the clays. CEC stands for cation exchange capacity. **Table S2:** Statistical comparison of the fraction of OC of soil-derived, natural organic matter (NOM) in solution in treatments with and without ion addition (H1). The table shows the *p* value of comparison of two treatments by student's *t* test. **Table S3:** Statistical comparison of the fraction of OC of soil-derived, natural organic matter (NOM) in solution in treatments with cations, and with and without inositol-hexaphosphate (IHP) addition (H3). The table shows the *p* value of comparison of two treatments by student's *t* test. **Table S4:** Statistical comparison of the fraction of OC of soil-derived, natural organic matter (NOM) in solution in treatments with clay minerals and goethite. The table shows the *p* value of comparison of two treatments by student's *t* test. **Table S5:** Statistical comparison of the fraction of OC of inositol-hexaphosphate (IHP) in solution in treatments with and without cations. The table shows the *p* value of comparison of two treatments by student's *t* test. **Table S6:** Statistical comparison of the fraction of OC of inositol-hexaphosphate (IHP) in solution in treatments with clay minerals and goethite (H4). The table shows the *p* value of comparison of two treatments by student's *t* test.